ECOLOGIE DE LA DYNAMIQUE DE FISSION-FUSION CHEZ LES SINGES ARAIGNÉES (*Ateles geoffroyi*)

par

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ECOLOGY OF FISSION-FUSION DYNAMICS IN SPIDER MONKEYS (*Ateles geoffroyi*)

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SOMMAIRE

Pour un individu, la vie en groupe a des avantages, mais aussi des coûts, selon la variabilité environnementale et les caractéristiques sociales du groupe comme la taille et la composition. La disponibilité des ressources alimentaires, qui peuvent varier dans le temps comme dans l'espace, est un élément important pour les animaux sociaux. La dynamique de fission-fusion réfère à la division temporaire d'un groupe en sous-groupes de tailles et de compositions différentes. Les changements en taille et composition de ces unités sont des réponses aux variations dans la qualité et quantité des ressources alimentaires. Jusqu'à présent, l'étude de la dynamique de fission-fusion s'est concentrée sur des variables écologiques et sociales comme la ségrégation. Des questions importantes restent à élucider et des incohérences entre les études persistent, notamment sur comment les sous-groupes répondent à l'interaction entre ces deux types de variables. La présente thèse traite de la dynamique de fission-fusion en considérant chacune des variables écologiques et sociales ainsi que leurs interactions. L'objectif principal est donc de comprendre l'influence relative de l'environnement et des variables sociales sur la dynamique de fission-fusion chez les singes araignées (*Ateles geoffroyi*).

Pour le développement de la thèse, j'ai obtenu des informations de deux groupes au Chiapas et un groupe au Yucatan. Les données des sous-groupes ont été récoltées à l'aide d'échantillonnage par balayage instantané. Au Chiapas, les observations ont été récoltées pendant une année (2014-2015) pour faire un total de 1604 heures de balayage instantané. Au Yucatan, les observations ont été faites pendant trois périodes de 12 mois: août 2009 à juillet 2010; janvier à décembre 2013, et janvier à décembre 2014, pour un total de 3235 heures de balayage instantané. La disponibilité des arbres fructifiant et sa variance proviennent de données phénologiques mesurées le long de transects dans l'aire vitale de chaque groupe.

En premier lieu, j'ai analysé comment les caractéristiques sociales d'un groupe (c.-à-d. la taille et la proportion de femelles) ainsi que les taux de fission varient dans l'espace

et le temps, suivant les précipitations et la disponibilité des arbres fructifiant. J'ai ainsi comparé deux habitats contrastés en termes de taille et de distributions des arbres, et des précipitation annuelle. Selon mes prédictions, les sous-groupes augmenteraient en taille et auraient une composition mixte pendant les périodes de plus haute disponibilité d'arbres fructifiant, de plus grande variance dans la disponibilité de ces arbres, et de plus forte précipitation. J'ai aussi prédit que le site de forêt tropicale sempervirente (en contraste avec le site de forêt tropicale saisonnière) supporterait des sous-groupes plus grands, plus mixte et que le taux de fission y serait plus faible. J'ai trouvé que la taille des sous-groupes est influencée par la disponibilité et la variance des arbres fructifiant, mais de façon opposée dans les deux sites. De plus, les taux de fission changent dépendamment des précipitations, encore une fois en sens inverse selon le site. La composition des sous-groupes n'a pas changé avec l'environnement.

En second lieu, j'ai étudié comment la synchronie comportementale dans les sous-groupes varie avec la disponibilité des arbres fructifiant, la taille des sous-groupes, la proportion des femelles, et l'heure de la journée. J'ai aussi testé comment la disponibilité des arbres fructifiant, la cohésion spatiale et la composition sexuelle des dyades sont liées à leur synchronie comportementale. Ma première hypothèse ici était que la synchronie comportementale dans les sous-groupes et les dyades est liée à la disponibilité des arbres fructifiant, à la taille des sous-groupes et à la composition sexuelle. Ceci s'expliquerait par de possibles conflits d'intérêts à travers la compétition pour les ressources alimentaires à cause des différences d'activités, de diète, et des préférences sociales selon le sexe. Ma deuxième hypothèse était qu'une plus grande cohésion spatiale, et une composition sexuelle homogène permettraient la synchronie comportementale des dyades. J'ai trouvé que la disponibilité des fruits permet la synchronisation comportementale juste au niveau des sous-groupes. La taille des sous-groupes est une contrainte pour la synchronisation comportementale. La répartition des individus d'un sous-groupe par type d'activité (c.-à-d. alimentation, repos, déplacement) a varié selon l'environnement et les variables sociales du groupe sans tendance claire, et parfois, différemment pour chaque groupe. Par exemple, la

synchronie d'alimentation a augmenté avec la disponibilité des arbres fructifiant dans un groupe alors qu'elle a diminué dans l'autre. Finalement, j'ai trouvé que la synchronie comportementale a augmenté avec la diminution de la distance entre individus d'une dyade, surtout pour les mâles.

En dernier lieu, j'ai analysé dans quelle mesure les patrons d'association (au niveau du sous-groupe) et de proximité (au niveau de la dyade) répondent à la disponibilité et la variance des arbres fructifiant et dans quelle mesure ces patrons répondent aux différences entre les sexes. J'ai testé l'hypothèse que la disponibilité des arbres fructifiant et sa variation spatio-temporelle exerceraient une influence sur la cohésion spatiale des sous-groupes. Ma deuxième hypothèse était que l'influence de la disponibilité des arbres fructifiant et de sa variance sur les patrons de proximité serait négligeable pour des individus proches spatialement (au niveau des dyades). J'ai trouvé que les patrons d'association (au niveau du sous-groupe) répondent aux changements de disponibilité des arbres fructifiant et sont influencés par le sexe des individus, possiblement du fait des interactions entre les processus environnementaux et sociaux. Les patrons de proximité sont affectés de façon minimale par la disponibilité des arbres fructifiant. Ceci suggère que les variables sociales sont plus importantes que les variables environnementales pour la cohésion spatiale au niveau des dyades.

En résumé, pour les singes araignées, la dynamique de fission-fusion fait partie d'une stratégie de comportement flexible permettant de gérer les différences entre les individus d'un groupe, les fluctuations locales de l'environnement et les différences des habitats dans la distribution géographique de l'espèce. Comprendre le fonctionnement de la dynamique de fission-fusion, selon les différentes conditions environnementales et sociales, nous permet de comprendre l'évolution et la flexibilité des dynamiques des groupes.

Mots clés: Dynamique de fission-fusion, singes araignées, *Ateles geoffroyi*, taille de sous-groupe, composition de sous-groupe, proportion de femelles, disponibilité des fruits, saisonnalité, habitats, synchronie d'activités, cohésion spatiale, association, proximité.

ABSTRACT

Living in groups can bring both benefits and costs to individuals depending on environment variability and group social characteristics, like size and composition. For animals, food availability is one important feature of the environment that varies across temporal and spatial scales. Social animals adapt their behaviour to cope with such variability in their environment using various strategies. Fission-fusion dynamics (FFD) is the temporal division of a group into subgroups of varying size and composition. Those changes in subgroup size and composition are responses to changes in quality and quantity of food resources. Studies on FFD have typically focused either on ecological or on social variables like sexual segregation. Important questions and inconsistencies remain between studies about how subgroups respond to these two variable types interacting. This thesis considers both ecological and social variables interacting and addressing FFD in a variable environment. The main objective of this thesis is to disentangle the relative influence of environmental and social variables on FFD in spider monkeys (*Ateles geoffroyi*). To do so, I studied three groups of spider monkeys in Mexico: two groups in Chiapas, and one group in Yucatan. In each study site, data on spider monkey subgroups were obtained through instantaneous scan samples. In Chiapas, observations corresponded to one year (2014-2015) on two groups totaling 1604 hours of scan-samples. In Yucatan, observations correspond to three 12-month periods: August 2009 to July 2010; January to December 2013, and January to December 2014, totaling 3235 hours of scan-samples. Data for fruit availability and variability were obtained from phenological data in trails within the home range of each study group.

The first aspect of FFD I investigated in this thesis was how social characteristics in a group (i.e. subgroup size and proportion of females) and fission rates in spider monkey subgroups vary in space and time with rainfall, and fruiting trees. I compared as well two contrasting habitats in terms of tree size and distribution, and annual precipitation. According to my predictions, subgroups would increase in size and have a mixed

composition during periods of higher availability of fruiting trees, greater variance in the availability of these trees, and higher precipitation. I also predicted that the evergreen forest site (in contrast to the seasonal tropical forest site) would support larger, more mixed subgroups, and that the fission rate would be lower. I found that the size of the subgroups is influenced by the variance of fruiting trees but in opposite ways in the two sites. In addition, fission rates change with precipitation, again in the opposite direction depending on the site. The composition of the subgroups has not changed with the environment.

Secondly, I evaluated how behavioral synchrony in subgroups varies with the availability of fruiting trees, size of subgroups, proportion of females, and the time of day. I also tested how the availability of fruiting trees, spatial cohesion and sex composition are related to behavioral synchrony. My first hypothesis was that behavioral synchrony in subgroups and in dyads is related to the availability of fruiting trees, subgroup size, and sexual composition because of possible conflicts of interest through foraging competition due to sexual differences in activity budgets, diet, and social preferences. My second hypothesis was that the greater spatial cohesion, and a homogeneous sexual composition would allow the behavioral synchrony in dyads. I found that fruit availability allows behavioral synchronization in subgroups but not in dyads. Subgroup size is a constraint for behavioral synchronization. The proportion of individuals in a subgroup by type of activity (i.e. feeding, resting, and traveling) varied according to the environmental and social variables of the group with no clear trends, and differently for each group. For instance, feeding synchrony increased with the availability of fruiting trees in one group while it decreased in the other. Finally, I found that behavioral synchrony increased with the decrease in the distance between individuals of a dyad, especially for males.

In my last chapter, I examined to what extent do association (at the subgroup level) and proximity patterns (for individuals in a dyad at close inter-individual distances) respond to the availability and variance of fruiting trees and at what extent, these patterns respond to differences between sexes. I hypothesized that fruit availability and

spatial-temporal variation of fruiting trees would influence the spatial cohesion of subgroups. Furthermore, differences between sexes would influence association and proximity patterns. My second hypothesis was that the influence of the availability of fruiting trees and its variance on local patterns would be negligible for spatially close proximities (at the dyad level). I found that association patterns (at the subgroup level) respond to changes in the availability of fruiting trees and are influenced by the sex of individuals, possibly due to the interaction between environmental and social processes. Proximity patterns were only minimally affected by the availability of fruiting trees. This suggests that social variables are more important than environmental variables for spatial cohesion at the dyad level.

In summary, for spider monkeys, fission-fusion dynamics are part of a flexible behavioral strategy to cope with differences between the individuals in a group, with a locally fluctuating environment and with differences between habitats within the geographic distribution of the species. Understanding the functioning of FFD under different environmental and social conditions could allow us to understand the evolution and flexibility of dynamics in groups.

Keywords: Fission-fusion dynamics, spider monkeys, *Ateles geoffroyi*, subgroup size, subgroup composition, habitats, behavioural synchrony, spatial cohesion, association, proximity.

RESUMEN

La vida en grupo trae consigo beneficios y costos a sus miembros dependiendo de la variabilidad del ambiente y de las características sociales del grupo como su tamaño y composición. La disponibilidad de recursos alimentarios que pueden variar a escalas temporal y espacial es un elemento importante para los animales sociales. La dinámica de fisión-fusión es la división temporal de un grupo en subgrupos de tamaño y composición variables, y esta dinámica está relacionada con los cambios en calidad y cantidad de los recursos alimentarios. Hasta el momento, los estudios de la dinámica de fisión-fusión se enfocan ya sea en variables ecológicas o en variables sociales como la segregación sexual. Aunque bien estudiada, aún permanecen preguntas e inconsistencias entre estudios especialmente sobre cómo los subgrupos responden a estas dos variables en interacción. En esta tesis considero variables tanto ecológicas como sociales interactuando. El principal objetivo de esta tesis es comprender la influencia relativa de las variables ambientales y sociales de la dinámica de fisión-fusión en los monos araña (*Ateles geoffroyi*).

Para el desarrollo de esta tesis, estudié tres grupos de monos araña en México: dos en Chiapas y uno en Yucatán. En cada sitio de estudio, realicé muestreos instantáneos de barrido en subgrupos de monos araña. En Chiapas, las observaciones se realizaron durante un año (2014-2015), sumando 1604 horas de muestreos de barrido. En Yucatán, las observaciones corresponden a tres periodos de 12 meses: agosto 2009 a Julio 2010; Enero a Diciembre 2013, y Enero a Diciembre 2014, sumando 3235 horas de muestreos de barrido. Los datos para la disponibilidad de frutos y su variabilidad fueron obtenidos de senderos fenológicos en el ámbito hogareño de los grupos.

El primer aspecto de la DFF que investigué en esta tesis fue cómo las características sociales de un grupo (i.e. tamaño y proporción de hembras) y la frecuencia de fisiones en subgrupos de monos araña, varían espacial y temporalmente en términos de precipitación y la disponibilidad de árboles con frutos. Esto, además, en dos hábitats contrastantes en términos de precipitación anual, y de distribución y tamaño de los

árboles con fruto. Predije que el tamaño de los subgrupos aumentaría y que su composición sería mixta a mayor disponibilidad de árboles con frutos, mayor varianza de dicha disponibilidad, y a mayor precipitación. También predije que habría subgrupos más grandes y mixtos, así como menos frecuencias de fisiones en el bosque tropical perennifolio (en contraste con el sitio del busque tropical estacional). Encontré que el tamaño de subgrupos varió con la disponibilidad y la varianza de árboles con frutos pero de manera opuesta en los dos sitios. Además, las tasas de fisión variaron con la precipitación, pero también en sentido inverso entre los sitios. La composición de los subgrupos no cambió con el ambiente.

En segundo lugar, evalué las relaciones entre la disponibilidad de frutos, el tamaño de subgrupos, la proporción de hembras y la hora del día, con la sincronización comportamental. También evalué cómo la disponibilidad de árboles con frutos, la cohesión espacial y la composición sexual, están relacionados con la sincronía comportamental a nivel de díadas. La primera hipótesis aquí fue que la sincronía comportamental en subgrupos y en díadas está relacionada con la disponibilidad de árboles con frutos, con el tamaño de los subgrupos y con su composición sexual debido a diferencias sexuales en la distribución de actividades, dieta y preferencias sociales. Mi segunda hipótesis fue que una alta cohesión espacial y que una composición sexual homogénea permite la sincronía comportamental en díadas. Encontré que la sincronización comportamental a nivel de subgrupos aumentó con la disponibilidad de árboles con frutos, pero disminuyó en la sincronización de díadas. El tamaño de subgrupo fue una restricción para la sincronía comportamental. La proporción de individuos de un subgrupo por tipo de actividad (i.e. alimentación, descanso, viajes) respondió de manera distinta con las variables ambientales y sociales, sin tendencia clara y en ocasiones en sentido opuesto en los dos grupos estudiados. Por ejemplo, la sincronía en alimentación aumentó con la disponibilidad de árboles con frutos en uno de los grupos y disminuyó en el otro. Finalmente, encontré que la sincronización comportamental aumentó con la disminución de la distancia inter-individual en las díadas, sobre todo entre los machos.

Por último, examiné hasta qué punto, los patrones de asociación (a nivel de subgrupo) y proximidad (a nivel de díadas) en la DFF responden a la disponibilidad y a la varianza de árboles con frutos, y hasta qué punto esos patrones se deben a diferencias entre sexos. La primera hipótesis aquí fue que la disponibilidad de árboles con frutos y su variación espaciotemporal ejercería una influencia en la cohesión espacial de subgrupos. Además, las diferencias entre los sexos podrían influir en los patrones de asociación y proximidad. También puse a prueba la hipótesis de que la influencia de la disponibilidad de árboles con frutos y su variabilidad sobre los patrones de proximidad, sería mínima a distancias cercanas entre los individuos (a nivel de díadas). Encontré que los patrones de asociación (a nivel de subgrupos) cambian con la disponibilidad de árboles con frutos y de acuerdo al sexo de los individuos indicando una interacción entre los procesos de ambientales y sociales. Los patrones de proximidad cambiaron mínimamente con la disponibilidad de frutos, lo que sugiere los factores sociales son más importantes que los factores ambientales para la cohesión espacial a nivel de díadas.

En suma, la DFF en monos araña es parte de una estrategia flexible de comportamiento para lidiar con las diferencias entre los individuos de un grupo, con el ambiente fluctuante a nivel local, y con las diferencias entre hábitats dentro de la distribución geográfica de la especie. Comprender el funcionamiento de la DFF bajo diferentes condiciones ambientales y sociales podría permitirnos comprender la evolución y la flexibilidad de la dinámica de grupos.

Palabras clave: Dinámica de fisión-fusión, monos araña, *Ateles geoffroyi*, tamaño de subgrupo, composición de subgrupo, proporción de hembras, disponibilidad de frutos, estacionalidad, hábitats, sincronía de actividades, cohesión espacial, asociación, proximidad.

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LIST OF ABBREVIATIONS

ECM	Ecological Constraint Model	Page 4
FFD	Fission-fusion dynamics	Page 1
IID	Inter-individual distances	Page 11
OMYK	Otoch Ma'ax Yetel Kooh	Page 21
MABR	Montes Azules Biosphere Reserve	Page 22
IFA	Index of Fruit Availability	Page 35
Variance_ft	Variance of fruiting trees	Page 46
CV	Coefficient of Variation	Page 36
DBH	Diameter at Breast Height	Page 41
SD	Standard Deviation	Page 45
S	Synchrony for all activities	Page 71
FS	Feeding Synchrony	Page 71
RS	Resting Synchrony	Page 71
TS	Traveling Synchrony	Page 71
M-M	male-male dyad	Page 73
F-F	female-female dyad	Page 73
M-F	male-female dyad	Page 73
AI	Association index	Page 115
P0	Association index at 0m of IID	Page 115
P5	Association index at 5m of IID	Page 115
CV_IID	Coefficient of variation of inter-individual distances	Page 115
Mod_Sex	Modularity by sex	Page 115
SAF	Strength of females to females	Page 115
SAM	Strength of males to males	Page 115
IFA_F	Index of fruit availability for *Ficus* spp.	Page 115
IFA_B	Index of fruit availability for *Brosimum alicastrum*	Page 115

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

GENERAL INTRODUCTION

Life in groups occurs in many animal species and involves behavioural strategies to increase the benefits and diminish the costs of this way of life. This thesis explores the fission-fusion dynamic (hereafter FFD), which is a flexible behavioural strategy, where changes in subgroup size and composition occur in response to changes in environment and resource availability to optimize foraging and protection against predators in groups, (Aureli *et al*., 2008). Here, FFD refers to the extent of variation in spatial cohesion (distances between the members of the group) and individual membership in a group over time (Aureli *et al*., 2008). These variations occur in response to changes in the environment and in the interests of individual group members (Sueur *et al*., 2011).

FFD is common in different animals like fishes (Wilson *et al*., 2014), birds (Loretto *et al*., 2017), and mammals (Aureli *et al*., 2008). In the case of mammals, FFD is present in modern humans, other primates such as chimpanzees and spider monkeys, dolphins, and bats (Aureli *et al*., 2008). Questions remain, however, regarding the mechanisms that drive the dynamics of flexible social groups, including the relative influence of social and environmental factors. For example, how do sizes of subgroups in a group, and the sex ratio of a group interplay? How does this relationship vary under different contexts of food availability? Does that relationship change according to the habitat contexts? How does FFD affect collective group behaviours like traveling or foraging at different social and spatial scales? Additionally, how spatial cohesion in groups is regulated by the environment considering sexual differences between individuals?

In this introductory chapter, I briefly provide first a review of the benefits and costs of living in groups. Secondly, I develop a framework for the Fission-fusion dynamics as a strategy for life in groups. Thirdly, I do a revision of the literature to provide information about how spatial cohesion can define groups and association patterns. Fourthly, I disentangle the role of the ecological and the social factors influencing this behavioural strategy. And lastly, I present behavioural synchrony as an indicator of group stability as part of the FFD. A better understanding of the mechanisms behind FFD, and how it relates to the environmental and the social factors of groups will give information about the ways social systems adapt to changes in the environment.

1.1 Benefits and costs of living in groups

Food acquisition is essential for survival, but animals often face a trade-off between obtaining energy when foraging, and competition problems or avoidance of danger predation (Stephens *et al*., 2007). Living in groups can partially offset this trade-off, for instance, when vigilance of others decreases each individual's need for vigilance allowing for higher individual feeding rates (Alexander, 1974; Davies *et al*., 2012). Additionally, group living can increase survival through predation avoidance, control of ecto-parasites through intra-specific grooming, and improve access, acquisition and cooperative defense of food sources (Chapman and Chapman, 2000b; Davies *et al*., 2012). Larger groups also face reduced threats from smaller potentially opposing groups of conspecifics (Alexander, 1974; Davies *et al*. 2012; Stander, 1992). However, living in groups can also be costly if there is high competition for scarce resources (Wrangham *et al*., 1993) or mates, and high group density can promote infection by pathogens (Alexander, 1974; Côté and Poulin, 1995; Davies *et al*., 2012).

Intra-group competition can reduce foraging efficiency in two ways: interference and scramble competition. Interference competition involves direct contests over food

resources, whereas scramble competition is the depletion of a limited resource through foraging and is independent of direct interaction with competitors (Nicholson, 1954; Wrangham *et al*., 1993). Interference and scramble competition can occur simultaneously (Davies *et al*., 2012). For example, scramble competition can occur at close distances between individuals, which may interfere with foraging behaviour (Krause *et al*., 2002). In that case, avoidance strategies and eventually escape performance to an eventual presence of interference competition can appear (Krause *et al*., 2002). An individual's foraging decisions may therefore be influenced by the number of potential competitors (Krause and Ruxton, 2002). In scramble competition individuals are forced to search more food patches (Wrangham *et al*., 1993). Thus, scramble competition likely restricts gregariousness and contributes to segregation in species with flexible group membership (i.e. species that present FFD) (Watts, 2005).

In addition to segregation, another consequence of increased scramble competition due to an increase in group size is that individuals are forced to visit more patches and cover greater areas than they would be required to do in smaller groups (Chapman *et al*., 1995). Another possible consequence of scramble competition is that the increase in the time and energy spent traveling eventually exceeds the energy obtained from food. Therefore, a smaller group should be advantageous (Chapman and Chapman, 2000a), if the costs of staying in a large group outweigh the benefits of leaving the group (Grove, 2012; Figure 1.1). Hence, there is a cost-benefit dilemma in group size (Sibly, 1983), which suggests that there might be an optimal size that maximizes an individual's fitness. As a consequence, group size is variable (Figure 1.1).

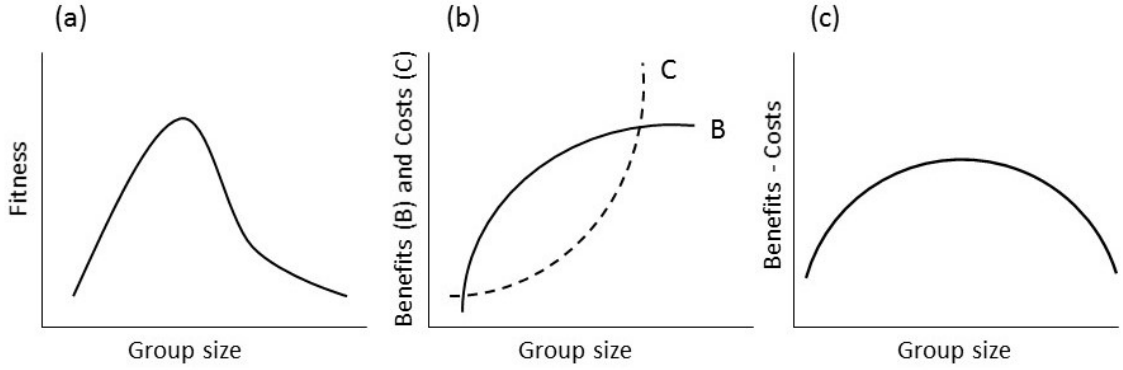

Figure 1.1. Optimal group size showing its fitness advantages, and its benefits and costs.

Optimal group size is expressed as (a) a hypothetical curve showing the fitness advantages obtained by individuals living in groups of different sizes. Above a certain number of individuals, the fitness advantages of joining a group decrease and individuals could decide to remain alone (After Sibly, 1983); (b) both benefits and costs increase as group size increases, but the increase in benefits will decelerate with each added individual, while the increase in costs will accelerate; therefore, costs will eventually exceed the benefits at large group sizes; (c) consequently, optimal size will occur theoretically at an intermediate group size. Sources for curves b) and c) are Krause and Ruxton (2002), Davies *et al*., (2012), and Grove (2012).

1.2 Ecological Constraint Model

Animals must forage over an area that can meet their energetic and nutritional requirements. Therefore, an increase in group size should increase the area that must be covered to find adequate food supplies (Milton, 1976; Chapman, 1990). The ecological constraint model (ECM) states that with an increase in group and subgroup

size, individuals can deplete food patches more rapidly, and are constrained to visit more patches and cover greater areas than they would be required to do in smaller groups (Chapman *et al*., 1995). This also means that individuals increase foraging effort and modify behaviors that are associated with food acquisition and energy conservation (Chapman *et al*. 1995, Wrangham *et al*., 1993). The ECM can be explained also from an environmental perspective, where ecological factors can influence movement patterns and foraging efficiency and thereby constrain (sub)group size (Chapman and Chapman, 2000b).

Chapman *et al*. (1995) proposed that food patch size, density and spatial distribution affect the movement patterns of animals in a group. According to these authors, the size of a food patch can limit the number of animals using the resource at the same time. The density of food patches can influence feeding efficiency by affecting inter-patch travel costs. Finally, the distribution of patches can similarly affect the distance travelled between a depleted patch and the next available food patch. Thus, larger groups should occur when patches are large, dense, and uniformly distributed, while smaller groups should occur in small, low density, and clumped patches (Chapman *et al*., 1995).

The ecological constraint model has been broadly studied in primates (e.g., Symington, 1988; Gillespie and Chapman, 2001; Lehmann *et al*., 2007, Asensio *et al*., 2009, Markham *et al*., 2017). It has also been used in studies on carnivorous mammals (e.g., Wrangham *et al*., 1993). The literature generally supports the ecological constraints model, but there are some inconsistent results. For instance, subgroups of capuchin monkeys did not respond to changes in food patch density and distribution (Chapman, 1990). Several authors found no correlation between subgroup size and daily range in chimpanzees (Lehmann and Boesch, 2004), *Procolobius badius* (Gillespie and Chapman, 2001), and *Brachyteles aracnoides* (Dias and Strier, 2003). One of the reasons for those inconsistencies is that there are many possible independent and

response variables to use, and various ways to measure them. The measurement of environmental variables is not always straightforward, and special attention regarding their interpretation has to be paid. For instance, even though Asensio *et al*. (2009) did not show an increase in travel time with subgroup size, they found that smaller subgroups visited both small and large food patches, whereas larger subgroups were constrained by the minimum patch size they could visit.

More recent studies on the ECM are adding the effects of group size on hormones indicative of stress (glucocorticoids in baboons, *Papio cyanocephalus*; Markham *et al*., 2017). These authors propose that beyond altering total foraging time and movement patterns, individuals in larger groups may mitigate the costs of intragroup competition by changing dietary preferences, foraging in lower-quality patches and/or increasing patch residence times. Other authors suggest that besides the balance of foraging costs to benefits, a constraint on time available to reach an energetic threshold could limit group subgroup size (Grove, 2012). Explorations around the ECM continues as it has a relationship with fitness and social organisation in animal groups.

1.3 Fission-fusion dynamics as a strategy for life in groups

Living in groups is a widely adopted life-history strategy that is of fundamental importance for many animal species (Davies *et al*., 2012; Krause and Ruxton, 2002; Sibly, 1983). Individuals in groups share benefits and interests (Conradt and Roper, 2000; Gravilets, 2015). For instance, relying on conspecifics for foraging, protection, or for the rearing of offspring is often essential for individual fitness in social animals (Davies *et al*., 2012). The fusion of individuals into social groups could permit an exchange of information and promote group behaviours such as collective decisions and behavioural synchrony. Indeed, social groups are often complex and may be composed of many individuals of different age and sex living together with different

levels of spatial cohesion and association between group members (Conradt and Roper, 2000; Gavrilets, 2015). For instance, in spatial cohesion, individuals in a group can be at different distances, and when close enough they can be considered in association, (Krause *et al*., 2009), or part of the same group or subgroup (Whitehead, 2008). Furthermore, interactions between associated individuals of different age and sex can be positive (i.e. grooming), or negative (i.e. aggressive interactions) and occur at different frequencies depending on the individuals involved (Hinde, 1976). The combined interactions between individuals of a group can lead to complex social relationships and determine the underlying social structure (Hinde, 1976; Wey *et al*., 2008).

Another important aspect of life in groups is the environment. When resources become scarce, increased competition between group members may reduce benefits of group living with high costs to survival and therefore on fitness (Davies *et al*., 2012; Sibly, 1983). Resource abundance can vary temporally as in seasonal environments, or spatially in or between landscapes, and FFD likely evolved as a behavioural strategy for social animals to respond to these changes in resources abundance (Sueur *et al*., 2011; Hartwell *et al*., 2018). The complexity of interactions between the spatiotemporal cohesion, group size, sexual composition and ecological variables constitutes the social organization (Kappeler and van Schaik, 2002). In such manner, FFD as a form of social organization reduces the potential costs of living in groups (Lehmann *et al*., 2007) by allowing individuals to reduce intra-group competition and improve foraging efficiency in spatially and temporally variable environments (Goldsmith and Winkler, 1999; Sueur *et al*., 2011). This strategy is related to the concept of fluidity as a measure of how often subgroup composition changes over time (Smith *et al*., 2008). In other words, FFD is the extent of variation in spatial cohesion and individual membership (subgroup size and composition) in a group over time to improve foraging efficiency (Aureli *et al*., 2008, Sueur *et al*., 2011). When the costs of maintaining a cohesive group becomes too high because of low resources or conflicting interests between individual

group members, a group can temporarily split into smaller subgroups and then recombine in larger subroups or again in the group when conditions improve. This fission-fusion aims to reinstate a balance between the costs and benefits of group living (Aureli *et al*., 2008; Sueur *et al*., 2011). The ecological constraint model (ECM), suggests that species with high levels of FFD should form smaller subgroups when access to resources requires longer travel distances (i.e., when small patches of resources are widely distributed) (Chapman *et al*., 1995). Hence, fission of the group into smaller subgroups reduces the costs of moving and thereby more energy can be allocated to feeding and social interactions (Lehmann *et al*., 2007).

Sueur *et al*. (2011) propose different scenarios of the relationship between spatial and temporal food availability with FFD. They propose that maintaining groups of individuals with different requirements should be highly costly if spatial variability of resources in the environment were very high in terms of quantity and distribution. Essentially, fission into several subgroups should occur if the costs outweigh the benefits of staying in a larger subgroup, whereas fusion or stability of a large subgroup is favored if the benefits of group living outweigh the costs. Hence, the FFD can be considered a feed-back loop (Figure 1.2). Therefore, larger heterogeneous subgroups should segregate into smaller, more homogeneous subgroups (i.e., individuals with similar requirements), in heterogeneous landscapes. The optimal composition of social groups in terms of age structure, sex ratio, ranges in body size, or genetic or social affiliation varies greatly between species and environments. For instance, hermit crabs (*Coenobita compressus*) form subgroups according to the structure of potential new shells in the space (Bates and Laidre, 2018); but other animals, like macaque species (*Macaca mulata* and *M. tonkeana*) split and form subgroups according to their affiliative relationships (Sueur *et al*., 2010), Bechstein's bats (*Myotis bechsteinii*) benefit from cooperation and communal breeding, which promotes long-term social bonds and explains their stable community membership (Kerth *et al*., 2011) despite the potential for FFD in this species. Other examples are that captive barnacle gees (*Branta*

leucopsis) are more likely to forage in groups with related individuals (Kurvers *et al*., 2013); and that in Common eiders (*Somateria mollisima*) the members of the subgroups arriving back at the colony are more related to each other than the colony average (Mckinnon *et al*., 2007). Hence, depending on resource availability and distribution in the landscape, subgroups should fuse together. In some species, subgroups should fuse besides when genetic or social affiliations are strong, and fission into small subgroups is more likely in the case of strong biological differences between individuals. Animal species can present low or high levels of FFD. For instance, a low level of FFD refers to very cohesive groups or constantly dispersed situations (e.g., territorial, solitary species) (Aureli *et al*., 2008). An intermediate level of FFD would include cases with a high variability in spatial cohesion and subgroup size but not in subgroup composition (i.e. hamadryas baboons) (Aureli *et al*., 2008). Finally, high levels of FFD present high variability in the spatial cohesion, in the subgroup size and in the subgroup composition (i.e. communities of chimpanzees, spider monkeys, and spotted hyenas) (Aureli *et al*., 2008).

In summary, FFD is a strategy seeking a temporal ideal subgroup size and composition for efficiency in foraging and protection from predators. Social affinities and biological differences in groups interact with food availability and its temporal and spatial variability. Those interactions lead to fusions in the case of social affinities and to fissions in the case of strong biological differences. Individuals in a same subgroup will be at different inter-individual distances that constitute spatial cohesion and that permit information exchange, and eventually collective decisions and behavioural synchrony in the subgroup. At this point, the environmental variables could influence ecological constraints (use of the space and intra-group competition), leading again to fission if the costs outweigh the benefits of staying in the subgroup, or to fusion or stability if benefits outweigh the costs of being part of the subgroup. In this case, the FFD can be considered a feed-back loop (Figure 1.2).

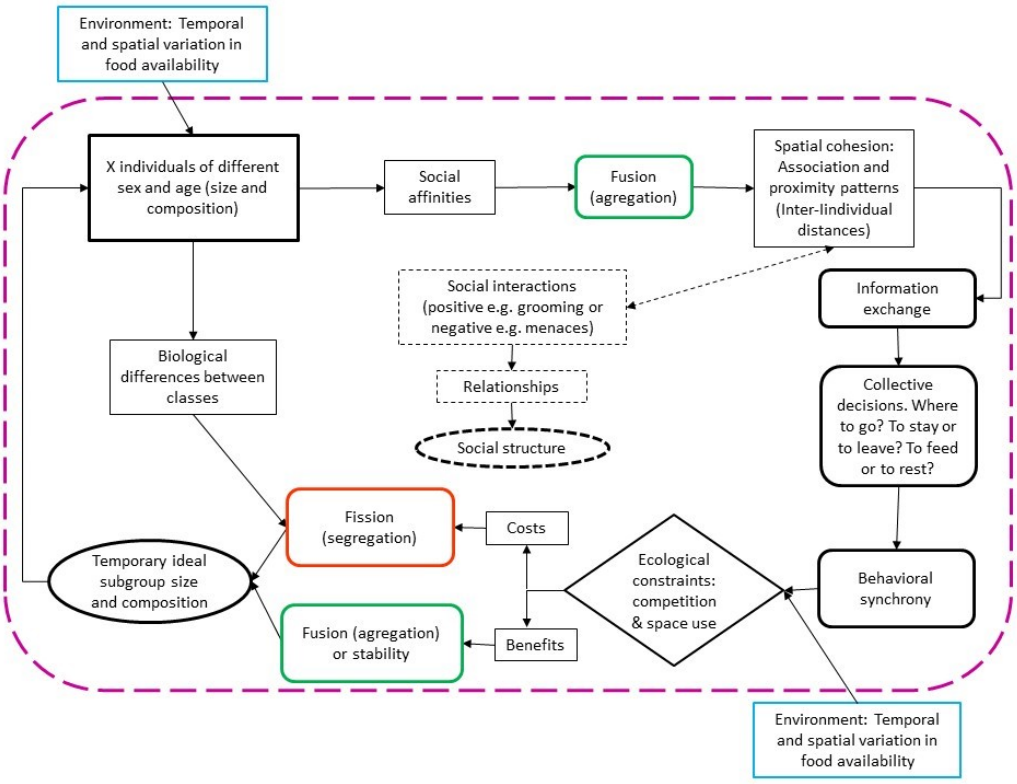

Figure 1.2. Diagram exemplifying the fission-fusion dynamics as a behavioural strategy for the social organisation in spider monkeys (*Ateles geoffroyi*).

The starting and ending point is a hypothetical and temporarily ideal subgroup size and composition (oval) leading to different subgroup sizes and compositions constrained by ecological factors (diamond). These constraints could eventually lead to processes such as fission or fusion in subgroups through information exchange, collective decisions and behavioural synchrony (smoother rectangles). The environment, social affinities, biological differences, and spatial cohesion are factors (rectangles) related directly or indirectly to subgroup membership, leading also to processes of fission, fusion, and behavioural synchrony. The broken rectangles and ovals are factors mentioned throughout the introduction as

part of the social organisation, but that do not form a direct relationship with the variables evaluated in this thesis.

1.4 Spatial cohesion defining group and association patterns

Spatial cohesion results from the variation of distances (IID) among individuals in a group (Whitehead, 2008. Inter-individual spacing occurs at different degrees, and relatively short inter-individual distances leads to spatial cohesiveness of the group, which is an important element of the social structure for a group because it permits coordination and information exchange (Krause *et al*., 2002; Sugiura *et al*., 2011). For instance, individuals staying close to one another are more likely to take the same travel routes and visit the same food patches than individuals far from other group members. Thus, the degree of spatial cohesiveness can also influence communication within a group, which is important for collective decisions such as choosing a patch or initiating a foraging journey (King and Cowlishaw, 2009; Sueur *et al*., 2011; Sugiura *et al*., 2011) including the performance of activities at unison (i.e. behavioural synchrony, King and Cowlishaw, 2009).

In this sense, it is important to distinguish between aggregations and social groups of individuals. An aggregation is the presence of many individuals of the same species in response to some non-social forcing factor, such as a localized source of food or shelter (Whitehead, 2008). According to Whitehead (2008), social groups result, however, from the active behaviour of individuals converging on or maintaining proximity with other individuals. Mechanisms for the recognition of conspecifics, familiar individuals, and in some cases of kinship, allow animals to selectively form those social groups (Krause *et al*., 2002; Smith, 2014). Within a group, individuals may also derive some benefit from actively seeking out or maintaining proximity with certain other individuals (Whitehead, 2008). Hence, once a group has formed, the inter-individual distances

between group members are the result of attraction and repulsion between individuals (Krause *et al*., 2002). Several techniques have been developed for determining what constitutes a group and a subgroup. For example, the shared use of resources such as feeding or nesting sites, roosts, and islets, is often used in defining groups (e.g. Bechstein's bats, Kerth *et al*., 2011; and birds, Loretto *et al*., 2017). Another way is the chain rule, which states that individuals are considered to be in the same subgroup when they are within a certain distance (x body lengths or x meters) from the next nearest individual (e.g. spider monkeys; Ramos-Fernández, 2005), plus perhaps participation in a similar behavioural state (Whitehead, 2008). Clusters produced by nearest-neighbor or clustering analyses on spatial arrangements of individuals have also been applied to determine group composition (Whitehead, 2008). Here, I use an empirical approach to define subgroups by measuring IID and by examining their distribution. By measuring inter-individual distances, it can be assumed that spatial proximity implies social affiliation considering that individuals must be in close physical proximity to interact (Pinter-Wollman *et al*., 2014).

In this thesis, I use the term association as a proxy for social groups under the assumption that physical closeness of two group members reflects social affinities between these individuals (Couzin, 2006; Ward *et al*., 2005, Krause and Ruxton, 2002). Two individuals are in association usually when interactions take place, but as interactions are more difficult to measure, associations are considered as state measures, and are used to obtain a quantitative measure of association or preference between individuals within a group (Whitehead, 2008). Here, association is given by the presence of individuals in a subgroup resulting from the FFD, and by their IIDs with respect to others in the subgroup (Whitehead, 2008). Association requires individuals to be within a range of communication because it involves the active or passive transmission of information that may influence the behaviour of the recipient (Bradbury and Vehrecamp, 1998). Associations in groups also imply an assortative behaviour given by individual preferences that can be highly variable in time (Krause and Ruxton

2002, Kerth *et al*., 2011). One can ask whether individuals with a certain characteristic preferentially interact with others who are similar to them with respect to this characteristic. If they do, then this is referred to as assortative pattern (Newman, 2003). Association and assortative patterns between subgroup members also vary with the costs and benefits of group living and are related to competition for resources (Aureli *et al*., 2012; Couzin, 2006; Krause and Ruxton, 2002; Madden *et al*., 2009).

In the FFD all individuals have the potential to interact with all others (James, *et al*., 2009), and the direct and indirect associations between individuals provide information about the connectedness of the social dynamics. Two major factors have been considered to affect group cohesiveness: predation avoidance and intragroup feeding competition (Sugiura *et al*., 2011). It has been suggested that avoidance behaviour has evolved to ensure that animals keep sufficient space between each other to facilitate efficient escape performance if a danger arises (Krause *et al*., 2002). Group cohesion can also be influenced by food distribution and seasonality (Sugiura *et al*., 2011, Hartwell *et al*., 2018). But also, inter-individual distance regulation can be under motivational control (Krause *et al*., 2002) meaning that social tendencies, predisposition, preferences and homophily can be present (Ruckstuhl and Neuhaus, 2000; Machado *et al*., 2019). It can be inferred that relative close distances between individuals in the same subgroup indicate tolerance, affiliation and negligible intra-group feeding competition. Even more, social preferences can be seen among individuals in other times than foraging, showing that homophily can be present during some behaviors (i.e. dolphins, *Tursiups truncatus*; Machado *et al*., 2019). On the contrary, relatively large distances between individuals have been interpreted as dispersion because of avoidance behaviour indicating scramble competition (Pinter-Wollman *et al*., 2014). Hence, the optimal IID is a trade-off between costs of close association with conspecifics, such as competition for resources, and benefits of being near preferred others, such as reduced risk of predation (Krause *et al*., 2002). In this

thesis, I address the environmental factors related to intragroup feeding competition and not with predation.

Another factor to consider for spatial cohesion are the performed activities. The activities in which individuals are engaged should therefore be considered when determining the IID required to include or not an individual in a subgroup (Sugiura *et al*., 2011). IID is often shorter when individuals are engaged in resting and grooming since they are often in physical contact with one another, and IID is longer during travels (Sugiura *et al*., 2011). IID is intermediate during foraging, since short distances between foraging individuals could interfere with typical foraging behaviours and increase competition, which can ultimately lead to individuals leaving the group or the disbanding of the entire group (Krause *et al*., 2002).

1.5 Ecological and social factors influencing FFD

Costs and benefits of living in group can depend on ecological (i.e. food availability and distribution; Chapman et al. 1995) or social factors (i.e. subgroup size and composition; Krause and Ruxton, 2002). When groups make decisions, the costs and benefits of the decision outcomes, for the individuals and for the group as a whole, often depend on the state of the environment. For example, local weather and food yields, predation risk, and optimal travel routes can influence how behavioural decisions affect survival in the short-term and fitness in the long-term. Incomplete and noisy information about the state of the environment can cast uncertainty on possible decisions faced by group members (Conradt and List, 2009). Grove (2012) states the importance of the quality and distribution of food patches to the ECM, affirming that if resource patches offer low energetic benefit or are dispersed they will be of little use to large groups.

In nature, food availability varies temporally and spatially, and some animals respond to changes in food availability by joining or leaving groups of conspecifics through processes of aggregation and segregation (Henzi *et al*., 2009, Pinter-Wollman *et al*. 2014; Ramos-Fernández *et al*., 2009). Density and sizes of food patches can vary along continuums from low to high, while patch distribution can vary from uniform to clumped (Chapman *et al*. 1995) and along geographical gradients (Kamilar and Baden, 2014). Some empirical studies have shown the importance of patch size and food abundance (Asensio et al., 2009; Chapman *et al*. 1995; Hartwell *et al*., 2014; Janson and Goldsmith, 1995; Korstjens *et al*., 2006; Itoh and Nishida, 2007; Rimbach *et al*., 2014; Smith *et al*., 2008; Stevenson *et al*., 1998; Strier, 1992). For instance, larger and more abundant food patches allow the formation of larger subgroups than smaller, sparsely distributed food patches (Asensio *et al*., 2009; Chapman *et al*. 1995; Janson, 1988; Janson and Goldsmith 1995; Strier, 1992). In seasonal environments, periods of low food availability can exert a strong limit on group size (Korstjens *et al*. 2006). Indeed, subgroups are usually larger during seasons of food abundance and smaller during seasons of food scarcity (Asensio *et al*., 2009; Chapman *et al*., 1995; Itoh and Nishida, 2007, Smith *et al*., 2008; Stevenson *et al*., 1998; but see Hartwell *et al*., 2014; Matthew et al., 2014; and Rimbach *et al*., 2014).

Segregation may also result from social factors such as group size and differences among individual traits (i.e. body size and reproductive state). Group members of different sex, age or physiological state are likely to have different energy or environmental requirements, which often lead to different interests (Conradt and List, 2009). Social segregation occurs in monomorphic species and in species with low dimorphism (i.e. squirrel monkeys, *Saimiri oerstedi*; Watts, 2005) as well as in species with high dimorphism (i.e. mandrills, *Mandrillus sphinx*; Watts, 2005). Some highly dimorphic species form stable mixed-sex groups (macaques, *Macaca fuscata*; Watts, 2005), however. The social preference between individuals can also influence sex-based aggregation or segregation (Social preference hypothesis, Bourgoin, 2018;

Ruckstuhl and Neuhaus, 2000). Aggregation according to social preference hypothesis occurs when individuals of the same sex or age class are more likely to interact with one another than with individuals of the opposite sex or of different age classes (Bourgoin *et al*. 2018; Ruckstuhl and Neuhaus, 2000). Association in same-sex groups could provide opportunities for developing social skills, and for males, the development of skills needed for success in mating competition. Watts (2005) suggests that the social preference hypothesis probably explains social and spatial segregation in some species like chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles* spp.). Thus, aggregation or segregation in a group can be affected by interactions between environmental and social factors.

In the next chapters of the thesis I use seasonality, food availability and differences between habitats as environmental factors affecting FFD. I also use subgroup size, female proportion and sex of the individuals as social factors also affecting the FFD. In each chapter, I try to disentangle the interplay of both environmental and social factors on this behavioural strategy.

1.6 Behavioural synchrony and stability of groups

Life in groups requires behavioural synchrony, meaning that individuals perform activities in unison (King and Cowlishaw, 2009). A group can be spatially coherent if its members synchronize activities such as foraging and resting (i.e. behavioural synchrony; Bourgoin *et al*., 2018; Conradt, 2005). Since group coordination often requires group decisions, group decision-making is likely to be important in most animal societies, as it is in human societies (Conradt and Roper, 2005; Kerth *et al*., 2006). Many social animals collectively decide group activities with important fitness consequences to all individuals (Conradt and List, 2009; Dostalkova and Spinka, 2007) through coordinated group movements, baby-sitting, sentinel behaviour and

cooperative foraging (Couzin and Krause, 2003; Whitehead, 1996). For instance, primate groups need to coordinate group activities and travel together if they are to accrue the protection and benefits of sociality (King and Sueur, 2011).

The contagious nature of certain kinds of behaviour may have evolved as a mechanism for achieving activity synchronization within social groups and, hence, maintaining group stability (Conradt and Roper, 2000). According to the hypothesis of allelomimesis, if there is a tendency for an individual to copy its neighbour's behaviour (i.e. feeding), then the greater the group size, the higher the probability that an individual will have a neighbour realising that activity (Deneubourg and Goss, 1989; Pays *et al*., 2007). However, to synchronize activities with other group members, an individual may have to compromise its own activity budget, entailing a cost (Conradt, 1998; Conradt and Roper, 2000). Thus, it could be expected that group members would act more synchronously in smaller and more homogeneous groups than in larger and mixed-sex groups because of distance between individuals and sex-based behavioural differences (King and Cowlishaw, 2009; Ruckstuhl, 1999; Pays *et al*., 2007).

The distribution of synchronization costs between group members depends on how homogeneous members are with respect to their optimal time budgets (Conradt, 1998; Conradt and Roper, 2003). The optimal allocation of time to various activities is likely to differ between sexes and age classes, and activity synchronization can have high costs and be difficult to achieve among members of different classes. Thus, variability in sex and age structure can cause group instability and even segregation if differences in time budgets between different classes are too high (Conradt, 1998; Conradt and Roper, 2000; Hartwell *et al*., 2014; Ruckstuhl 1999; Ruckstuhl and Neuhaus, 2000). Differences in behavioural synchrony within all-male and all-female groups imply that additional factors other than sex-based differences in foraging rhythm contribute to the instability in mixed-sex groups (Conradt, 1998). 'Conflicting interests' (Conradt and List, 2009) describe when different decision options, carrying different ranks importance, are

favoured according to the pay-offs for individuals with different traits. Unreliability of information and conflicting interests may occur simultaneously in nature (Conradt and List, 2009) making it difficult to maintain high cohesion (spatial coordination) and behavioural synchrony (temporal coordination) across all group members (Conradt and Roper, 2007).

1.7 Importance of the study

Fission-fusion dynamics are important in understanding how conspecific associations affect survival and reproductive success in most social species. However, aspects of this behavioural strategy such as variation of subgroup size and subgroup composition, segregation, and mechanisms for coordinating group behaviour are still unclear to ecologists. Furthermore, quantitative analyses of how FFD are affected by environment interplaying with the trait and social characteristics of group members is still lacking. Inconsistencies in our current understanding of these phenomena may be caused by environment variability through time, between regions and within the distribution of animal species (Kay *et al*., 1997; Korstjens *et al*., 2006; Sueur *et al*. 2011). As a consequence, environmental variability can result in variability in food availability, which in turn could result in variability in social organisation. Thus, current knowledge of the mechanisms of FFD and the ways in which ecological and social factors interact to influence FFD is still relatively undeveloped.

Long-term studies of primates reveal considerable flexibility in grouping patterns and within-group social relationship, both between and within populations of higher-FFD taxa over time (Aureli *et al*., 2008). Furthermore, it is important to consider the different social scales (i.e. dyad, subgroup and group) studied since as FFD is related to spatial cohesion of the individuals in a group. Different social scales could provide different information on the mechanisms driving behavioural strategies for social organisation.

Considering that the FFD is a very flexible behavioural strategy, I investigated the importance of considering habitat characteristics, in the context of different social scales when conducting socio-ecological observations for behavioural studies. I also identify the importance of considering differences in foraging rhythms between sexes and individual reproductive state in the case of species with sexual segregation like spider monkeys.

This thesis will contribute important insight into the mechanisms explaining grouping patterns, dispersal tendencies, and inter- and intra-sexual social relationships as adaptive responses to the ecological and social environment (Aureli *et al*., 2008). Results from my thesis will clarify our understanding of the mechanisms and adaptation of social structure in social mammals, and ultimately, of the evolution of social systems (Conradt and Roper, 2007; Kerth *et al*., 2011; Ramos-Fernández *et al*., 2006, Sueur *et al*., 2011). In addition, as spider monkeys are endangered by habitat loss (IUCN, Cuarón *et al*., 2008), this study will provide information about the possible limits in the behavioural plasticity of this species under different environmental conditions, including disturbed habitats.

1.8 Study species: the spider monkey (*Ateles geoffroyi*; Kuhl, 1820)

Spider monkeys (Figure 1.3) occur primarily in lowland rain forest, evergreen, semideciduous, and deciduous forest, mostly traveling and foraging in the upper levels of the canopy (Cuarón *et al*., 2008). The geographic distribution of spider monkeys spans Belize, Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, and Panama. Some large areas of suitable habitat still exist, but severe habitat loss across its natural range has resulted in a decline of as much as 50% over the last 55 years (three generations). Therefore, the spider monkey is listed as

Endangered in the International Union for Conservation of Nature (IUCN, Cuarón *et al*., 2008).

Spider monkeys are the largest bodied Mesoamerican primates. Males weight 7.4–9.0 kg (mean = 8.3 kg), while adult females weight 6.0–9.4 kg (mean = 7.7 kg) (Cuarón *et al*., 2008; Garber *et al*., 2005). Females produce their first infant at 7–9 years old, have a long 226–232 day gestation, and an interbirth interval of approximately 3 years (Garber *et al*., 2006). The genus *Ateles* presents high cognitive abilities compared to other New World genera (*e.g. Cebus sp*.) and some Old-World genera (*Pongo*, *Pan* and *Gorilla*, Deaner *et al*., 2006). Cognitively complex organisms are more likely to present FFD (Couzin, 2006).

Fruits are the most common food item in the spider monkey's diet (39–94%), followed by leaves (6–55%), flowers (0–29%), and other plant parts and insects (0–14%; González-Zamora *et al*., 2009). Spider monkeys prefer plants from the Moraceae and Fabaceae families. The most important factor that influences spider monkey ranging behaviour and habitat use is the availability and distribution of fruit resources in the forest (Valero and Byrne, 2007). Ripe fruits are particularly important because of their seasonal variation in production (Valero and Byrne, 2007).

Spider monkeys form groups of 15–55 individuals (Shimooka *et al*., 2008), which are divided into subgroups of up to 30 monkeys (Ramos-Fernández *et al*., 2011). The average size of a foraging spider monkey subgroup is relatively small compared to group size (Chapman *et al*., 1995), and different subgroups may occupy different areas of the group's home ranges, especially during periods of fruit scarcity (Shimooka, 2003). Group composition in the genus *Ateles* is generally female-dominated (Shimooka *et al*., 2008). Nevertheless, the sex ratio (M:F) is variable across sites and in time within the same site. For example, in Barro Colorado Island, sex ratio changed

in one year from 1:5 to 6:1. This could be due to development of individuals, mortality rates and migrations.

In this genus, female dispersal occurs (Shimooka *et al*., 2008). Communities of spider monkeys have been described as sex-segregated for two main reasons. First, females frequently travel alone or in small groups with offspring, but also travel in larger groups with females or with males when food is abundant. Second, they display less frequently affiliative behaviours than males (i.e. grooming), so they are considered “less social” than males (Aureli and Schaffner, 2008). Males also have larger core areas and spend more time traveling, while females spend more time feeding (Symington, 1988; Wallace, 2008). The longer time allocated to traveling and the larger core areas in males are thought to be related to territorial defense and patrolling of boundary areas of their home range (Wallace, 2008).

Figure 1.3. Adult male spider monkey (*Ateles geoffroyi*).

1.9 Study areas

Fieldwork took place in two areas within the current distribution of spider monkeys in Mexico. Sites had different types of vegetation and climatic conditions (Figure 1.4). The first area was the protected forest of Otoch Ma'ax Yetel Kooh (OMYK; 20°38′ N, 87°38′ W, 14-m elevation), on the Yucatan Peninsula. Here, the mean annual temperature is 24.3 °C and mean annual rainfall is 1120 mm (1951–2010; Servicio Meteorológico Nacional, 2015). OMYK is dominated by several successional stages of medium semi-evergreen forest (García- Frapolli *et al*., 2007). Mature stands are dominated by fruit-bearing species such as Mayan breadnut or ramón (*Brosimum alicastrum* Sw.), sapodilla or zapote (*Manilkara zapota* [L.] P. Royen), and the álamo fig tree (*Ficus maxima* Mill.). Late successional stages are stands that are 30–50 years-old and include important species, such as black poisonwood or chechén (*Metopium brownei* Roxb.) and Jamaican dogwood (*Piscidia piscipula* [L.] Sarg.). Earlier successional stages include species such as gumbo-limbo or chacá (*Bursera simaruba* [L.] Sarg.), and tox'ok (*Caesalpinia gaumeri* Greenm.) (García-Frapolli *et al*., 2007).

The second study area lies 610 km south of OMYK, in the Montes Azules Biosphere Reserve (MABR; 16°05′58″ N, 90°52′36″ W, 10–50-m elevation) in the state of Chiapas. Mean annual temperature is 24.0 °C, and mean annual rainfall is 2881 mm SEMARNAP 2000), more than twice that of OMYK. The native vegetation of the site in MABR is predominantly tropical evergreen forest. Fruit-bearing species that are common include gumbo-limbo, Mayan breadnut, sapodilla, and jutahy or palo lacandón (*Dialium guianense* [Aubl.] Sandwith.) (SEMARNAP, 2000). Differences in vegetation between the two study sites are not only a consequence of climate, but also of soil characteristics and biogeography.

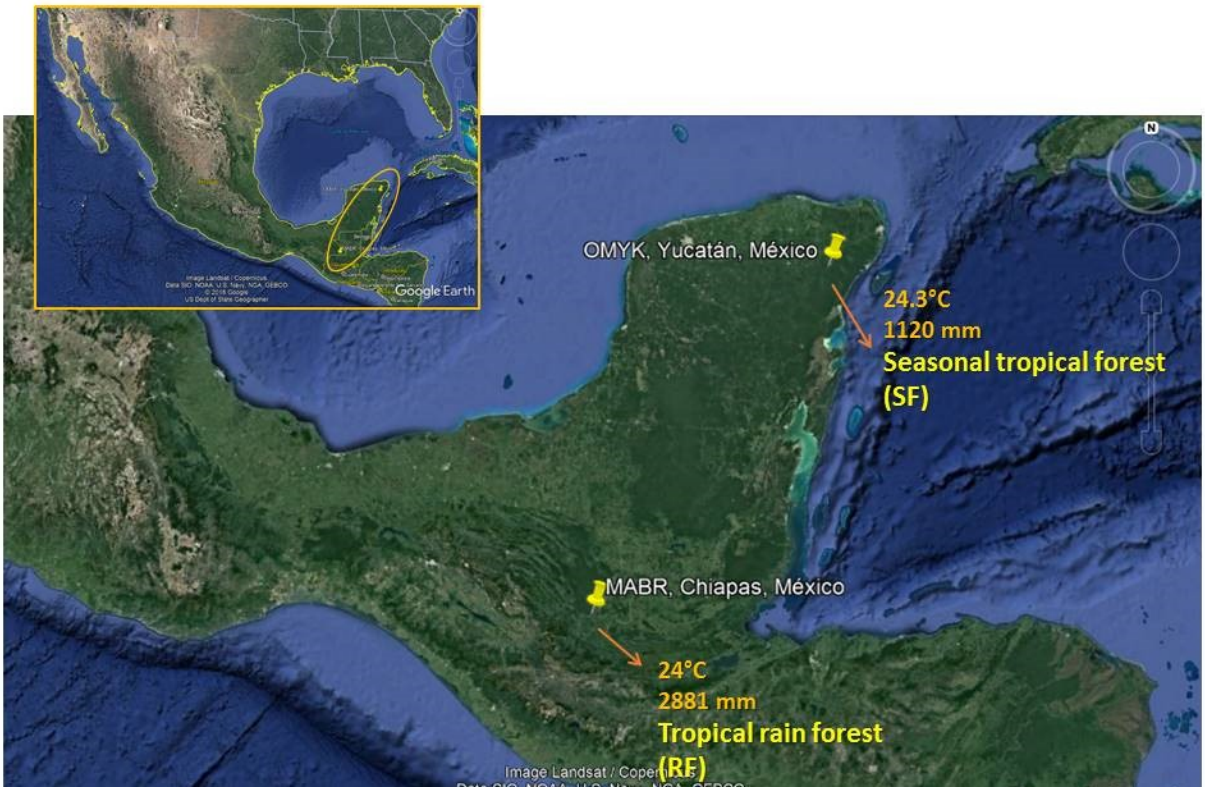

Figure 1.4. Map of the two study sites where the spider monkeys were studied, Otoch Ma'ax Yetel Kooh (OMYK) in Yucatán, and the Montes Azules Biosphere Reserve (MABR) in Chiapas.

Google Earth (December 13, 2015). OMYK 20° 50' 25.38'' N, 87° 33' 53.66'' W, Eye alt 1636.41 km. MABR 16° 16' 09.46'' N, 90° 56' 24.13'' W, Eye alt 1636.41 km. SIO, NOAA, U. W. Navy, GEBCO, Google 2018, INEGI 2018.

1.10 Objectives and thesis structure

The main objective of this thesis was to disentangle the relative influence of environmental (i.e. fruit availability) and social variables (i.e. subgroup size, sex of individuals and female proportion) on the FFD in spider monkeys. The variables that I

included in my research are subgroup size, sexual composition in subgroups (i.e. the proportion of females), fission rates, behavioural synchrony, and spatial cohesion through association and proximity patterns. In addition, I included different temporal, regional, and social scales (i.e. dyads and subgroups).

Specifically, I addressed the following questions:

1. How do size, composition, and fission rates of subgroups of black-handed spider monkeys change with food availability and its variance? The study was conducted in two sites that are located in different types of habitat which exhibit contrasting conditions of rainfall, and food distribution and availability (Chapter 2);

2. How is behavioural synchronisation affected by food availability, subgroup size, and the proportion of females in subgroups, as well as energetic needs throughout the day in spider monkeys? (Chapter 3);

3. How is behavioural synchronisation affected by spatial cohesion, fruit availability and sex-class in dyads? (Chapter 3);

4. To what extent does FFD change to passive aggregation processes due to fruit availability and variability? To what extent does FFD respond to active aggregation processes due to differences between sexes? And to what extend passive and active aggregation processes interplay on the FFD? I investigate these effects at two levels of social organisation; dyads and subgroups. (Chapter 4)

To respond to these questions, this document is organised into three chapters each one constituting a scientific article. The first article (Chapter 2) addresses the influence of the environment at both temporal and regional scales on subgroup size, female proportion in subgroups and fission rates. I compared these relationships in two different areas characterised by different types of vegetation and different climatic conditions. In the second article (Chapter 3) I tested the extent to which environmental, social and internal factors modify behavioural synchrony in spider monkeys as an indicator of group stability and FFD. I included feeding synchrony, resting synchrony, traveling synchrony, and also synchrony of all these activities together. In Chapter 3 I also tested how inter-individual distances, as a proxy of information transfer, and sexual composition, influenced behavioural synchrony. For the third article (Chapter 4) I investigated the extent to which spatial cohesion of spider monkeys, through association and proximity patterns, varies passively due to fruit availability, and actively due to social factors (i.e. sex of individuals). Figure 1.5 shows the organization of the objectives in my thesis.

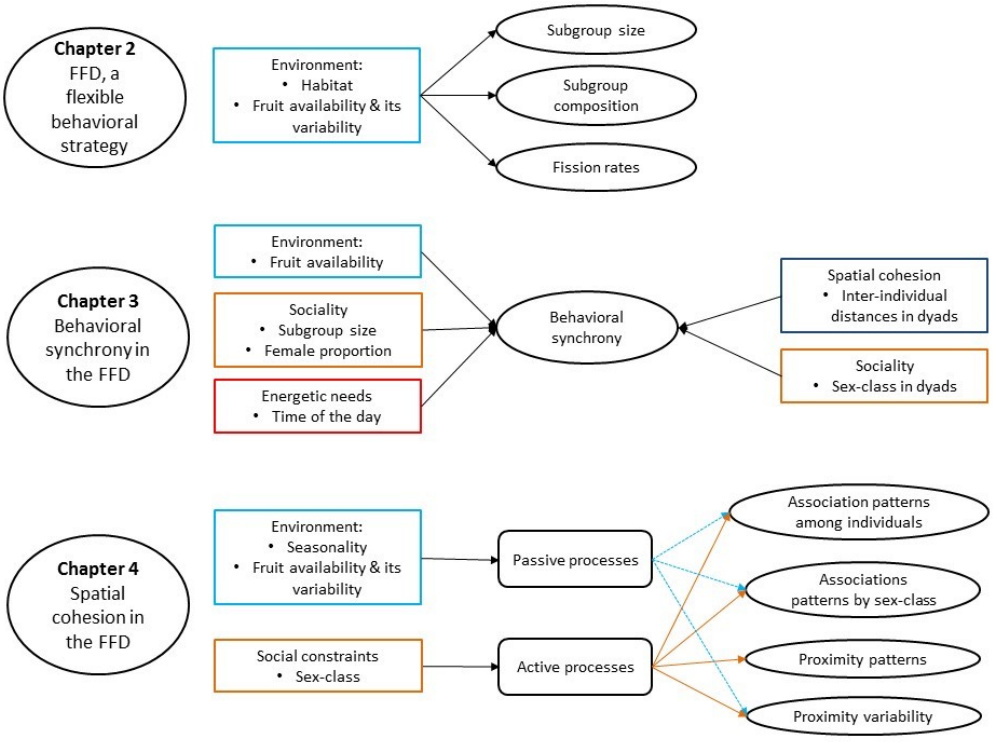

Figure 1.5. Organization of my main study objectives and thesis chapters.

This figure shows the hypothesis concerning the relative influence of environmental and social variables (blue, orange and red rectangles) on factors related to the FFD (ovals) in spider monkeys (*Ateles geoffroyi*).

CHAPTER 2

FISSION-FUSION DYNAMICS AS A TEMPORALLY AND SPATIALLY FLEXIBLE BEHAVIORAL STRATEGY IN SPIDER MONKEYS

2.1 Description of the article and contribution

FFD is characterized by changes in membership (number of individuals and composition) of subgroups and in spatial cohesion of a group. This chapter, corresponding to the first objective of the thesis, shows how variables related to FFD (subgroup size, composition and fission rates) vary over time with environmental variables such as rainfall, fruit availability and its variability. In this chapter we also address the relationships of FFD-related variables with the patterns of spatial distribution of two important food species for spider monkeys. Finally, we compare the responses for two vegetation types. Our results show how flexible can be the FFD as behavioral strategy; but also, how habitat characteristics influence responses. Even when this study comprises only two study sites such studies comparing sites with different biotic and abiotic characteristics remain rare, and our results might explain the inconsistencies found among studies regarding the responses of membership in groups to food availability.

For this article, I proposed the idea, and it was improved with the help of Sophie Calmé, Sandra E. Smith-Aguilar, and Gabriel Ramos-Fernández. I collected the data in MABR with the help of field assistants. Gabriel Ramos-Fernández, Filippo Aureli, Colleen Schaffner and Laura Vick, who run a long-term project at OMYK, provided the data for this site. Sandra E. Smith-Aguilar and I prepared the databases needed for the statistical analyses. I performed the statistical analyses, after previous discussion with

Sophie Calmé and Gabriel Ramos-Fernández. Audrey Bourret and Sandra E. Smith-Aguilar helped many times with important details in the statistical analyses. Sophie Calmé, Sandra E. Smith-Aguilar and Gabriel Ramos-Fernández reviewed several versions of the manuscript and discussed with me in many occasions to give a better shape to the final manuscript.

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Fission-fusion dynamics as a temporally and spatially flexible behavioral strategy in spider monkeys

Adriana R. Aguilar-Melo, Sophie Calmé, Sandra E. Smith-Aguilar, Gabriel Ramos-Fernandez

2.2 Abstract

Fission-fusion dynamics (FFD) encompass a behavioral strategy present in many animal species that reduces the costs and increases the benefits of group living. In this case study, we investigated how group characteristics (size and composition) and fission rates in spider monkeys varied in space and time with rainfall, fruit availability, and it variability in two sites, each presenting different characteristics regarding the distribution and size of food patches and rainfall. Habitat characteristics strongly influenced FFD in spider monkeys, particularly subgroup size and fission rate. Subgroup size varied with fruit availability and its variability, while fission rates varied with rainfall and fruit variability. However, both subgroup size and fission rate varied in opposite ways, depending upon habitat type. Subgroups tended to present stable mixed-sex composition regardless of fruit availability. We conclude that for spider monkeys, FFD are part of a flexible behavioral strategy to cope with a locally fluctuating environment and with different environments within the geographic range of the species.

2.3 Significance statement

Fission-fusion dynamics (FFD) constitute a form of social organization that allows some species to take advantage of living in groups under different environmental conditions.

The relationship between social organization and environmental variables has been well studied, but inconsistencies remain. One potential reason for these inconsistencies may be the focus of most studies on a single habitat type, with few formal comparisons of FFD in the various habitats occupied by a species. We evaluated how habitat characteristics (e.g., food availability and rainfall) affect FFD (assessed through subgroup size, subgroup composition, and fission rate) in spider monkeys (*Ateles geoffroyi*) in two different habitat types. We found that within a single habitat type, food availability, variability, and rainfall affected subgroup size and fission rate. Crucially, these relationships contrasted sharply, depending on habitat type. Our study shows that FFD are flexible within and across habitats, indicating the importance of considering habitat characteristics when conducting socio-ecological observations. We caution against generalizations based upon single-habitat studies.

Keywords Subgroup size. Subgroup composition. Behavioral plasticity. Food availability. Habitat characteristics, *Ateles geoffroyi*.

2.4 Introduction

Many species have evolved behavioral strategies to maintain the benefits of group living while reducing its costs. One way to reduce intra-group feeding competition (one of the main costs of group living) and improve foraging efficiency in spatially and temporally variable environments is through high fission-fusion dynamics (FFD). These dynamics describe the way that animals organize themselves in space and time based on variation in group cohesion, size, and composition (Aureli et al. 2008; Sueur et al. 2011). FFD arise from a lack of consensus within the group, resulting in the segregation of group members according to their needs and characteristics (i.e., sex or age class, genetic, or social affiliation; Krause and Ruxton 2002; Sueur et al. 2011).

According to the ecological-constraints model (ECM), subgroup size and composition depend upon the environment and vary according to food availability and variability (Box 1984; Chapman et al. 1995; Aureli et al. 2008; Sueur et al. 2011). For instance, high food abundance and density, clumped distributions of food resources, and rainy seasons (reflecting food abundance) lead to the formation of larger subgroups in primates, carnivores, and ungulates (Wrangham et al. 1993; Chapman et al. 1995; Chapman and Chapman 2000; Itoh and Nishida 2007; Asensio et al. 2009; Bercovitch and Berry 2009). Yet, even when this relationship between group characteristics and environmental variables has been well studied, there are inconsistent results in many intra- and interspecific studies. For example, contrary to ECM expectations, Wolf et al. (2018) found no difference in group size for giraffes (*Giraffa camelopardalis*) when comparing between seasons of food abundance and scarcity. Likewise, group size in the Venezuelan red howler monkey (*Alouatta seniculus*) and variegated or brown spider monkey (*Ateles hybridus*) was negatively related to fruit patch density (Stevenson et al. 1998) and fruit availability (Rimbach et al. 2014), respectively, and there was no relationship at all for white-bellied or long-haired spider monkeys (*Ateles belzebuth*), tufted capuchins (*Cebus apella*), common woolly monkeys (*Lagothrix lagotricha*) (Stevenson et al. 1998), and common chimpanzees (*Pan troglodytes*) (Hashimoto et al. 2003). Newton-Fisher et al. (2000) found no relationship between subgroup size and food distribution in chimpanzees; Lehmann et al. (2007) and Hartwell et al. (2014) also found no association between subgroup size and fruit availability in chimpanzees, bonobos (*P. paniscus*), and black-handed or Geoffrey's spider monkey (*Ateles geoffroyi*), respectively (but see Janson 1988). In addition, Chapman et al. (1995) suggested that subgroups of spider monkeys and chimpanzees could be larger in clumped patches, even if patch size is small and patch density is low across the landscape.

Subgroup composition under high FFD can also vary according to food availability. So far, studies of changes in group composition have mainly focused upon sexual

segregation or aggregation of individuals (Conradt and Roper 2000; Krause and Ruxton 2002). One cause of sexual segregation relates to differences in the energetic requirements of individuals of each sex (Chapman 1990; Conradt and Roper 2000; Krause and Ruxton 2002; Hartwell et al. 2014). For instance, Chapman et al. (1995) predicted that subgroups of spider monkeys and chimpanzees would be more mixed in clumped patches, even if patches are small and scattered. Indeed, Hartwell et al. (2014) found that male and female spider monkeys tended to form mixed groups during periods of low food availability. On the contrary, Wolf et al. (2018) found more homogenous (i.e., multi-female and multi-male) groups of giraffes in winter, when food is scarce.

Sueur et al. (2011) provided different scenarios of temporal and spatial variability of food resources to explain FFD. These authors proposed that during periods of high temporal variability of food resources (i.e., high seasonality), FFD should increase. However, when food patches are scarce or highly unpredictable in time (i.e., changes in food availability are not predictable at a given time scale), individuals should reach high levels of consensus, thereby remaining in cohesive groups, lowering fission and fusion rates, and forming larger and more mixed groups (Sueur et al. 2011). When spatial variability increases (i.e., clumped patches), consensus costs (i.e., costs of making collective decisions) should also increase, leading to higher fission and fusion rates. These actions should result in partial or complete segregation of individuals into relatively more homogeneous subgroups that are composed of individuals with similar requirements (Krause and Ruxton 2002; Conradt and Roper 2007; Sueur et al. 2011). When individuals segregate because of high spatial variability of food or remain cohesive because of low spatial variability of food (i.e., homogeneous distribution), low fission and fusion rates are expected (Sueur et al. 2011). Finally, at intermediate degrees of spatial variability (e.g., when food patches vary in quality or quantity to an intermediate extent), a low rate of consensus in decision-making occurs and a high degree of FFD is expected. These scenarios and predictions point to contextual factors

of the environment that would influence FFD, with contexts varying across sites at a broader geographical scale.

Most empirical studies on FFD, particularly on changes in subgroup size, composition and cohesion have been carried out within one site or habitat type (e.g., Chapman et al. 1995; Stevenson et al. 1998; Itoh and Nishida 2007; Lehmann et al. 2007; Asensio et al. 2009; Rimbach et al. 2014; but see Bercovitch and Berry 2009). This might explain discrepancies between studies, since plasticity in behavior could imply different ways of coping with environmental variation across sites. Considering that habitat characteristics of a given species can vary across its geographic range, FFD could vary through space, as habitat type could be a selective force leading to behavioral variation and flexibility in social organization (Korstjens et al. 2006; Bercovitch and Berry 2009; Kamilar and Baden 2014). Therefore, as climate and food availability vary along geographical gradients (e.g., Kay et al. 1997), they are likely to influence FFD through geographical variation of social organization. For instance, Korstjens et al. (2006) tested the relationship between subgroup size and climate in spider monkeys, and found a positive linear relation with temperature and a quadratic one with rainfall peaking at intermediate values. Thus, we can expect that species exhibiting high FFD will display differences in their social organization, depending upon the contextual characteristics of the sites that they inhabit.

We present a case study in which we tested how size, composition, and fission rates in subgroups of black-handed spider monkeys changed with food availability and variability in space and time, in two sites that were located in different types of habitat exhibiting contrasting conditions of rainfall and food distribution and availability. The spider monkey is a good model species because it exhibits high variation in spatial cohesion, subgroup size, and composition (Aureli et al. 2008). We expected that rainfall and food availability and variability would all influence subgroup size (empirical studies, Chapman et al. 1995; Lehmann et al. 2007; Smith et al. 2008) and sex composition

(conceptual frameworks, Aureli et al. 2008; Sueur et al. 2011) (see Table 2.1 for predictions). Specifically, we expected subgroups to increase in size and have a mixed composition with greater fruit availability, variability, and rainfall (Janson 1988; Chapman et al. 1995; Sueur et al. 2011). We also expected greater food tree cross-sectional area (i.e., larger food patches) or food tree basal area (i.e., denser food patches) to support larger subgroups (Janson 1988; Chapman et al. 1995); moreover, clumped fruit patches should allow larger and more mixed subgroups than would homogeneously distributed fruit patches (Chapman et al. 1995). Lastly, based on the scenarios that were presented by Sueur et al. (2011), we expected fission rates to increase when rainfall or fruit availability decreased and when (or where) food resources had a clumped distribution or existed in smaller or less dense food patches (Smith et al. 2008; Sueur et al. 2011; Table 2.1).

Table 2.1. Definition and justification of explanatory variables used to quantify the influence of food availability on size and composition of subgroups, and on fission rate.

Explanatory variable and definition	Justification	Expectations		
		Subgroup size	Subgroup sexual composition	Fission rate
IFA: Fruit availability of the most consumed food species in the respective study site (see Methods)	Subgroup size and composition change with fruit availability (Chapman et al. 1995, Stevenson et al. 1998).	Increase with IFA (1, 2, 3)	~M at higher IFA (1, 2)	Decrease at higher IFA (6)
Variance-ft: Variance of fruiting trees of the more important food species for spider monkey in the study site (see Methods)	Represents heterogeneity in the foraging environment. Also related to the concept of variability in Sueur et al. (2011).	Increase with Variance-ft (2)	~M at higher variance-ft (2, 8)	Decrease at higher variance-ft, more so in MABR (8)
Rainfall: Precipitation (mm)	Used in some studies as indicator of food availability (Lehmann et al. 2007; Asensio et al. 2009). Both sites present differences in rainfall (Table 2.2).	Increase with Rainfall (5, 7)	~M at higher rainfall (1, 2)	Decrease at higher Rainfall (6)

Explanatory variable and definition	Justification	Expectations		
		Subgroup size	Subgroup sexual composition	Fission rate
Study Site: OMYK and MABR	Each site presents different characteristics (see Table 2.2).			
		Food tree-cross sectional area		
	Most studies have used food patch size measured as the size of a given food tree (Chapman et al. 1995; Newton-Fischer et al. 2000; Itoh and Nishida 2007; here, food tree cross-sectional area, cm^2);	OMYK < MABR (1, 2, 4, 5)	OMYK: ~H; MABR: ~M (1, 2)	OMYK > MABR (6)
		Food tree basal area		
	Studies have also used food patch size as the density of food trees (Stevenson et al. 1988; Chapman et al. 1995; Itoh and Nishida 2007; here, food tree basal area, cm^2/ha);	OMYK < MABR (2, 3, 5)	OMYK: ~H; MABR: ~M (2)	OMYK > MABR (6)
		CV of tree density		
	Other studies have used food distribution pattern (Stevenson et al. 1988: Chapman et al. 1995; Newton-Fischer et al. 2000; here, CV of tree density)	OMYK > MABR (2, 4, 5)	OMYK: ~M; MABR: ~H (2)	OMYK > MABR (8)

* Table 2.1. The last three columns show the expectations of the study. Subgroup composition tends to be homogeneous (~H) when values are closer to 0 (adult males only) or 1 (adult females only), and mixed (~M) when the proportion of females is closer to 0.5. Study site was added in the models as a categorical variable; here we show how different aspects of each site could influence FFD in different ways. Numbers within parentheses under each prediction indicate the corresponding references (listed below)

(1) Janson 1988; (2) Chapman *et al*., 1995; (3) Stevenson *et al*., 1998; (4) Newton-Fischer *et al*., 2000; (5) Itoh and Nishida, 2007; (6) Smith *et al*., 2008; (7) Asensio *et al*, 2009; (8) Sueur *et al*., 2011.

2.5 Material and methods

2.5.1 Study sites

We conducted fieldwork in two areas within the current distribution of *Ateles geoffroyi* in Mexico that were characterized by different types of vegetation and climatic conditions. The first area was the protected area of Otoch Ma'ax Yetel Kooh (OMYK; 20°38′ N, 87°38′ W, 14-m elevation), on the Yucatan Peninsula. Mean annual temperature is 24.3 °C, and mean annual rainfall is 1120 mm (1951–2010; Servicio Meteorológico Nacional 2015). Table S1 (in the supplementary online material) summarizes monthly rainfall (mm), mean monthly temperature (°C), and the minimum and maximum temperatures (°C) in OMYK during the field season. OMYK is dominated by several successional stages of medium semi-evergreen forest (García-Frapolli et al. 2007). Mature stands are dominated by fruit bearing species such as Mayan breadnut or ramón (*Brosimum alicastrum* Sw.), elemuy (*Malmea depressa* [Baillon] R.E. Fries), sapodilla or zapote (*Manilkara zapota* [L.] P. Royen), and the álamo fig tree (*Ficus maxima* Mill.). Late successional stages (stands that are 30- to 50-years-old) include important species, such as false tamarind (*Lysiloma latisiliquum* [L.] Benth.), black

poisonwood or chechén (*Metopium brownei* Roxb.), and Jamaican dogwood (*Piscidia piscipula* [L.] Sarg.). Earlier successional stages include species such as gumbo-limbo or chacá (*Bursera simaruba* [L.] Sarg.), and tox'ok (*Caesalpinia gaumeri* Greenm.) (García-Frapolli et al. 2007).

The second study area lies 610 km south of OMYK, in the Montes Azules Biosphere Reserve (MABR; 16°05′58″ N, 90°52′36″ W, 10–50-m elevation) in the state of Chiapas. Mean annual temperature is 24.0 °C, and mean annual rainfall is 2881 mm (SEMARNAP 2000), i.e., more than twice that of OMYK. Also see Table S1 for rainfall and temperature data recorded in MABR during the study period. The native vegetation of the site in MABR is predominantly tropical evergreen forest. Fruit-bearing species that are common include gumbo-limbo, Mayan breadnut, sapodilla, and jutahy or palo lacandón (*Dialium guianense* [Aubl.] Sandwith.) (SEMARNAP 2000). Differences in vegetation between the two study sites are not only a consequence of climate, but also of soil characteristics and biogeography.

2.5.2 Study groups

We studied one group of spider monkeys in OMYK over 2 years (2013 and 2014), and two groups in MABR over 1 year (2014–2015). The group in OMYK has been studied since 1997 as part of a long-term project (Ramos-Fernández et al. 2018). Both groups in MABR have been monitored since 1998 (R. Lombera, pers. comm., 27March 2015), resulting in habituation to humans. In OMYK, the group included 38 individuals (15 adult and sub-adult females, 7 adult and sub-adult males, and 16 young) in 2013 and 47 individuals (20 adult and sub-adult females, 9 adult and sub-adult males, and 18 young) in 2014. In MABR, one group had 19 individuals (9 adult and sub-adult females, 7 adult and sub-adult males, and 3 young) and the other group had 14 individuals (5 adult and

sub-adult females, 4 adult and sub-adult males, and 5 young). It was not possible to record data blindly because our study involved focal animals in the field.

2.5.3 Subgroup size, composition, and fission/fusion rates

In OMYK, four local field assistants (all working in the long-term project since 1998), one of us (SSA), and several other students collected the data. In MABR, two local field assistants, one of us (ARAM), and several students collected the data.

In OMYK, observation periods lasted 14 days per month, from January 2013 to December 2014. In MABR, observation periods lasted 6 to 8 days per month for each group from May to December 2014, and 14 days per month for each group from January to April 2015. Groups were followed 4–8 h per day between dawn and dusk, and instantaneous scan samples were taken every 20 min (Martin and Bateson 2007). Instantaneous scan samples and observation times totaled 2150 scan samples and 716 h in 2013, and 2665 scan samples and 888 h in 2014. In MABR, data collection totaled 934 instantaneous scan samples over 311 h of observation for group 1, and 796 instantaneous scan samples over 265 h for group 2.

During the instantaneous scans, we recorded subgroup size and composition. We followed the definition of subgroup that was used by Ramos-Fernández (2005) and validated by Aureli et al. (2012), i.e., all individuals that were observed at a distance less than or equal to 30 m from at least one current subgroup member that belonged to the same subgroup. Sexual composition of the subgroups was measured through the proportion of females (adult and sub-adult females/subgroup size; Ramos-Fernández and Morales 2014). Thus, ratings of 0 and 1 indicated homogeneous

subgroups (only males and only females, respectively), and 0.5 indicated perfectly mixed subgroups (equal number of females and males).

Fission and fusion events were identified when measuring subgroup size during the instantaneous scans. We considered a fission to have happened when one or more individuals from a given subgroup were not observed within that subgroup for two consecutive scans. Similarly, a fusion occurred when one or more individuals that did not belong to a given subgroup were observed within that subgroup, over two consecutive scans (Aureli et al. 2012). We obtained fission and fusion rates respectively by dividing the number of fission and fusion events by the number of observation hours per period. Given that fission and fusion rates were positively correlated ($r_s = 0.7$, $p < 0.001$, $n = 70$), we retained only the fission rates in subsequent analyses.

2.5.4 Food availability and distribution

We assessed the temporal variability of fruit availability on phenological trails running through the study groups' home ranges. In OMYK, the phenological trail was monitored every second week throughout the study period, recording the phenological status of 10 individuals of each of the top 10 food species according to records of the monkey's monthly diet between 1997 and 2004 (Pinacho-Guendulain and Ramos-Fernández 2017; Table A2 in the Supplementary online material). In MARB, phenological trails were monitored after every observation period for each group, i.e., once a month by registering the presence/absence of fruit on 10 individuals of each of the top eight food species. These species were the eight most important food species in continuous forest for spider monkeys at the site, according to records of their monthly diet in 2007 and 2008 (during three consecutive days once every 3 weeks; Chaves et al. 2012). In this earlier study, these eight species represented 80% of feeding time; however, they

represented only 57% in our study (Table A2 in the Supplementary online material). We also characterized the distribution and abundance of the top food species in both study sites (Table 2.1). We counted and measured the diameter at breast height (DBH, 1.3 m) of all individuals (DBH > 10 cm) of the most important food tree species in plots, calculated their density (number of stems/ha), cross-sectional areas ($\pi*(DBH^2/4)$; cm^2), and respective basal areas (cross-sectional area divided by sampled area; cm^2/ha). We also estimated the coefficient of variation of food tree density and basal area to define clumped (> 1) or uniform (< 1) distribution. In OMYK, those data were obtained from 48 random belt transects of 100 × 2 m (200 m^2) and eight square plots of 2500 m^2 each, in the activity area of the group, which summed to 2.96 ha (Pinacho-Guendulain and Ramos-Fernández 2017). In MARB, we obtained the data from 95 circular plots of 10-m radius (314.16m^2) in the activity area of each group (Rivera and Calmé 2006), totaling 2.99 ha per area.

To evaluate food availability for spider monkeys, which are highly frugivorous, we considered three variables, the index of fruit availability of the top food species (IFA), the variance of the number of fruiting trees of the top food species (variance-ft), and rainfall. The index of fruit availability (IFA) is the sum of the proportion of trees with fruit (out of 10) for each species and observation period, multiplied by the density (individuals/ha) and the sum of the DBH per hectare for each species (Smith-Aguilar et al. 2016). Variance of the fruiting trees (Variance-ft) is the statistical variance associated with the fruiting trees that were monitored every second week in the phenology transects. Rainfall data were collated and averaged over the same 2-week intervals that were used for sampling monkeys, using daily rainfall records from nearby meteorological stations (Servicio Meteorológico Nacional 2017). We used rainfall to characterize the study sites, because climate variables have been used as indicators of food productivity (e.g., very dry and very wet habitats, Lehmann et al. 2007; dry and wet seasons, Asensio et al. 2009; Korstjens et al. 2006).

2.5.5 Data analyses

We tested the differences of food tree density, food tree cross sectional area, food tree basal area, and biweekly rainfall between the study sites through Wilcoxon rank sum tests (Z values; Table 2.2). We tested the climatic differences between the study sites also with the Wilcoxon rank sum tests (Table S1).

We used generalized linear mixed models (GLMM) to test the relationships between subgroup size, proportion of females, and fission rate and the explanatory variables (study site, observation period, IFA, variance of the fruiting trees, and biweekly rainfall; Table 2.1). We fitted a Poisson distribution and log-link function for subgroup size and a binomial distribution with logit-link function for the proportion of females. Fission rate was normally distributed according to the Shapiro-Wilk test. We checked homoscedasticity by plotting residuals against predicted values and detected no pattern for any of the variables. We normalized all explanatory variables by subtracting the mean and dividing by the standard deviation. All the explanatory variables were used as fixed effects, except for observation period that was treated as a random effect. For each response variable, we considered all possible two-way interactions between explanatory variables.

Before running the models, we tested for collinearity among explanatory variables in two ways, by adding the data of both study sites together and separately by site. In the collinearity test with both study sites pooled together, there was no collinearity between fixed factors (IFA and variance of the fruiting trees: $r = 0.19$, IFA and biweekly rainfall: $r = 0.16$, variance of the fruiting trees and biweekly rainfall: $r = -0.09$, $n = 70$ in all the cases, $p > 0.05$ in all cases confirmed with Spearman correlations). When conducting collinearity tests by study site, IFA and variance of fruiting trees in MABR exhibited a correlation of 0.76 in the data for modeling subgroup size and proportion of females,

and of 0.74 in the data for modeling fission rate ($p < 0.001$ and $n = 70$ in both cases). In the Supplementary online material, we include Spearman rank correlations between the independent variables and the dependent variables (Fig. S2).

We fitted the models using the lme4 library (Bates et al. 2015) in R version 3.3.2 (R Core Team2016). To construct the most parsimonious models possible, we began with the saturated model (Tables S3–S5 in the Supplementary online material), and then used backward elimination to sequentially remove the variable with the highest *p* value, using the criterion $\alpha = 0.05$. We compared each new model to the previous one with a likelihood-ratio test (Bolker 2007). For fission rate (modeled using lmer function), we computed p values with the lmerTest package (Bates et al. 2015). We used the Akaike information criterion, corrected for small sample sizes (AICc; Burnham et al. 2011; Symonds and Moussalli 2011), to confirm what we found in the likelihood-ratio test.

2.6 Results

2.6.1 Characteristics of study sites

The two sites exhibited important differences in climatic conditions during the study (Fig. S1a in Supplementary online material), as well as differences in the abundance, cross sectional area, basal area, and distribution of the most important food tree species for spider monkeys (Table 2.2). Rainfall (mean biweekly rainfall) was twice as high in MABR as in OMYK, but present a lower coefficient of variation (OMYK: $\bar{x}$ = 51.89mm, coefficient of variation, CV = 1.05; MABR: $\bar{x}$ = 99.42 mm, CV = 0.99, Wilcoxon Z = 2819.5, p = 0.001). Important food trees in MABR were much larger, with a food tree cross-sectional area over five times that of important food trees in OMYK; the forest in MABR also presented a much larger food tree basal area, which was

almost five times that of OMYK. OMYK was more heterogeneous temporally and spatially than MABR (Table 2.2). In particular, fruit availability (in quantity; mean biweekly IFA) was higher and more variable in OMYK than in MABR (OMYK: IFA = 32,050, CV = 0.95; MABR: IFA = 7560, CV = 0.55; Wilcoxon Z = 336, p = 0.015; Fig. S1b,c in the Supplementary online material).

Table 2.2. Differences in the characteristics of the top food tree species and rainfall between the two study sites (OMYK and MABR).

Site variable	Study site			
			Z	*P*
	OMYK	MABR		
Tree density (stems/ha)	16.46 ± 21.53	14.51 ± 8.60	65	0.267
Food tree cross-sectional area (cm^2)	375.26 ± 581.98	2021.67 ± 3998.95	103830	<<0.001
Food tree basal area	6177.55 ± 9274.96	29085.43 ± 15945.02	16	<<0.001
CV (tree density)	1.31 (clumped)	0.59 (uniform)		
CV (food tree basal area)	1.50 (clumped)	0.55 (uniform)		
Biweekly Rainfall (mm)	51.90 ± 54.51	99.42 ± 98.21	2820	<<0.001

* Food tree cross-sectional area was calculated multiplying the π value with the squared DBH divided by 4 (formula = π•(DBH2/4), and basal area (cm^2/ha) was calculated by dividing cross-sectional area by the area of the food tree plots. Distribution is clumped if the Coefficient of Variance, CV (tree density) > 1 or uniform if < 1 (Sokal and Rohlf 2003), Error terms (±) are the standard deviation values.

2.6.2 Subgroup size

Subgroups were significantly larger in OMYK than in MABR (OMYK: $\bar{x}$ = 4 ± 2.8 SD; MABR: $\bar{x}$ = 2.6 ± 1.6 SD; Z = 4.766, p < 0.001; range 1–16 in both sites). Fruit availability (IFA) and the variance of fruiting trees affected subgroup size in opposite ways in the two study sites. Subgroup size responded as expected in OMYK, by slightly increasing

with increasing fruit availability, whereas in MABR, subgroup size strongly decreased with increasing fruit availability (Table 2.3, Fig. 1a). Conversely, subgroup size increased as expected with the variance of fruiting trees in MABR, whereas it slightly decreased in OMYK (Table 2.3, Fig. 1b).

Table 2.3. Parameters of the best model explaining subgroup size of spider monkeys at OMYK and MABR.

Independent variable	Estimate	SE	*Z*	*P*
(Intercept)	0.331	0.126	2.636	0.008
Site (OMYK)	*1.069*	*0.133*	*8.039*	*0.000*
IFA	*-1.280*	*0.207*	*-6.197*	*0.000*
Variance_ft	*0.233*	*0.048*	*4.852*	*0.000*
Rainfall	-0.044	0.036	-1.240	0.215
Site:IFA	*1.400*	*0.209*	*6.687*	*0.000*
Site:Variance_ft	*-0.283*	*0.063*	*-4.504*	*0.000*

* The best model: Subgroup size ~ Site + IFA + Variance_ft + Rainfall + Site×IFA + Site×Variance_ft + (1|Observation Period). Italic indicates variables with a significant effect. IFA = Index of fruit availability; Variance_ft = Variance of fruiting trees.

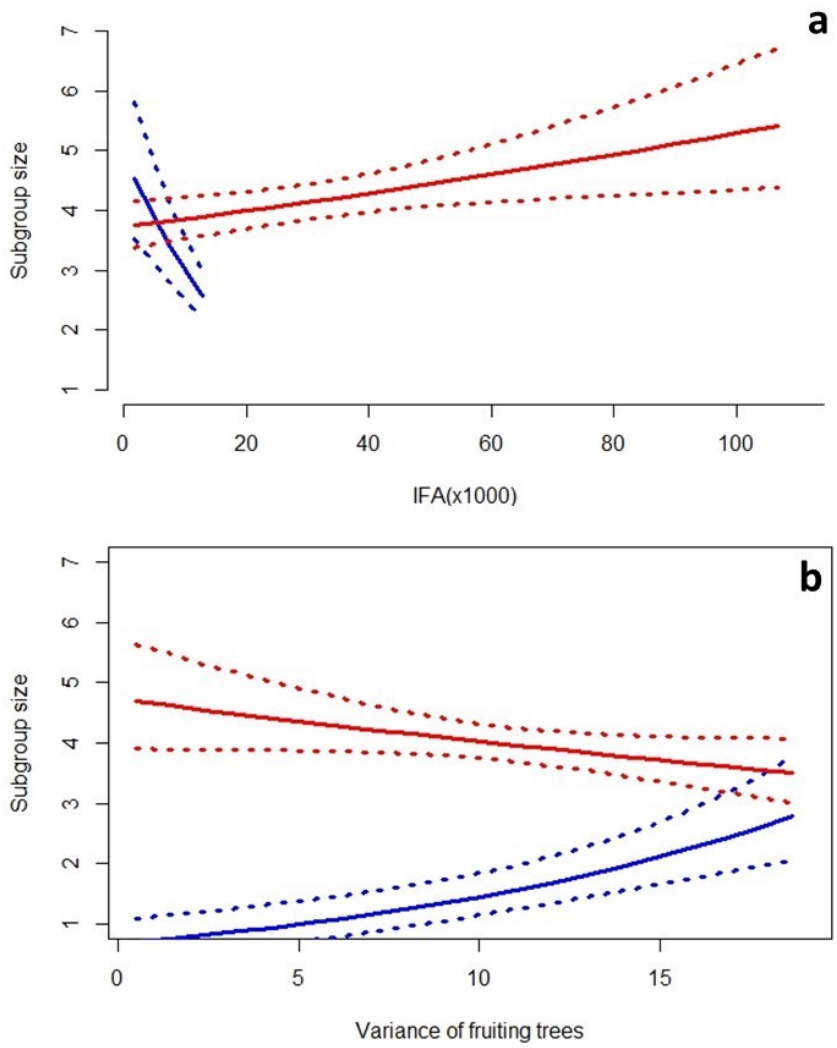


Figure 2.1. a Effect of fruit availability (IFA) on spider monkey subgroup size in each study site: OMYK (red line) and MABR (blue line). b Effect of variance of fruiting trees on spider monkey subgroup size in each study site: OMYK (red line) and MABR (blue line).

Lines represent the estimated effect of IFA on the response variable and dotted lines represent confidence bands (95%). Lines were obtained using the effects package (Fox 2003). Note that the maximum value of IFA in MABR was 160, 000.

2.6.3 Subgroup composition

The mean proportion of females in subgroups was 0.67 ± 0.38 SD in OMYK and 0.66 ± 0.37 SD in MABR. These values did not differ statistically between sites (Table 2.4) and indicated that subgroups were frequently mixed. The only change in the proportion of females was a weak but significant decrease when the variance of fruiting trees increased in both sites (Table 2.4).

Table 2.4. Parameters of the best model explaining the proportion of females in spider monkey subgroups at OMYK and MABR.

Independent variable	Estimate	SE	*Z*	*P*
(Intercept)	-0.505	0.115	-4.411	0.000
Site (OMYK)	0.048	0.133	0.359	0.720
IFA	0.022	0.045	0.489	0.625
Variance_ft	*-0.091*	*0.033*	*-2.775*	*0.005*
Rainfall	0.027	0.048	0.554	0.580

* Best model: Proportion of females ~ Site + IFA + Variance_ft + Rainfall + (1|Observation Period). Italic indicates variables with a significant effect. IFA = Index of fruit availability; Variance_ft = Variance of fruiting trees.

2.6.4 Fission rate

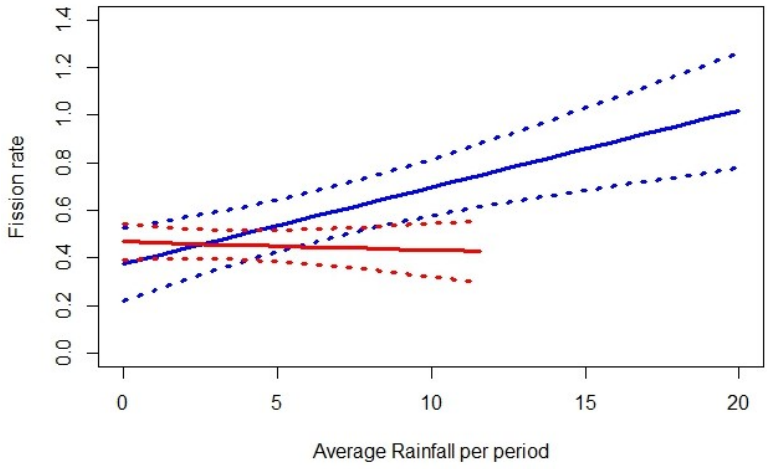
Fission rates did not differ between sites, but change with the interaction between study site and rainfall. As expected, fission rate decreased when rainfall increased, but only

in OMYK (Figure 2.2). In MABR, the opposite occurred, i.e., fission rate increased with rainfall (Figure 2.2). Fission rate also responded to the interaction between fruit availability and variability (i.e., IFA × Variance-ft). As expected, at high fruit availability, fission rate strongly decreased with increasing variance of fruiting trees (Figure 2.3). In contrast, subgroups tended to be more unstable at lower variance of fruiting trees with increasing fruit availability (Figure 2.3). Yet, subgroups tended to be more stable during low fruit availability, without regard for the variance of fruiting trees (Table 2.5).

Table 2.5. Parameters of the best model explaining the fission rate of spider monkey subgroups at OMYK and MABR.

Independent variable	Estimate	SE	*t*	*P*
(Intercept)	0.533	0.056	9.505	0.000
Site (OMYK)	-0.061	0.069	-0.892	0.376
IFA	*0.102*	*0.030*	*3.331*	*0.001*
Variance_ft	*-0.051*	*0.027*	*-1.892*	*0. 063*
Rainfall	*0.120*	*0.032*	*3.797*	*0.000*
Site:Rainfall	*-0.128*	*0.049*	*-2.628*	*0.011*
IFA:Variance_ft	*-0.089*	*0.030*	*-2.933*	*0. 004*

* Best model: Fission rate ~ Site + IFA + Variance_ft + Rainfall + Site×Rainfall + IFA×Variance_ft (1|Observation Period). Italic indicates variables with a significant effect. IFA = Index of fruit availability; Variance_ft = Variance of fruiting trees.



in each study site: OMYK (red line) and MABR (blue line).

Lines represent the estimated effect of rainfall on the response variable and dotted lines represent confidence bands (95%). Lines were obtained using the effects package in R (Fox 2003).

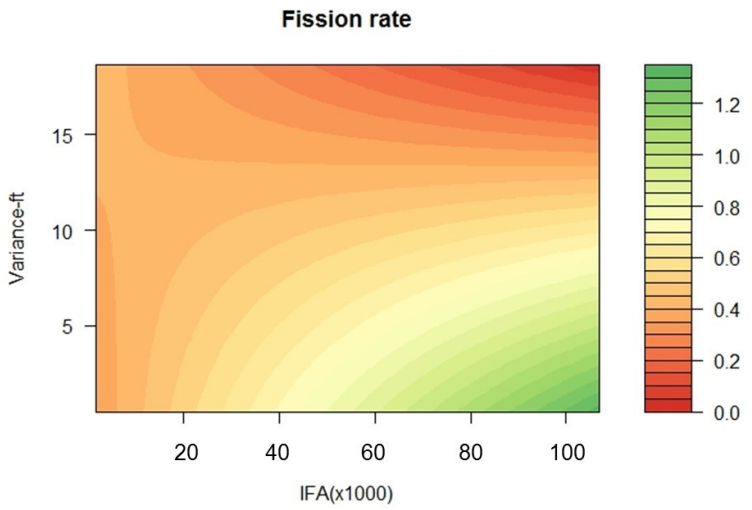


Figure 2.3. Conditional plot showing the effect of fruit availability (IFA) and its variability (variance-ft) on the fission rate of spider monkey subgroups in both study sites.

Fission rate values are shown as a gradient of colors.

2.7 Discussion

Our study was aimed at understanding how resource availability and its variability influence subgroup size, composition, and fission rate as components of fission-fusion dynamics. Our results show that changes in fruit availability influence FFD in spider monkeys, but also suggest that characteristics of the habitat are important because in one of the sites, the predictions related to fruit availability and its variability were supported, while those in the other site showed opposite tendencies.

2.7.1 Subgroup size

Subgroup size was affected by food availability, although in different ways, depending on the habitat characteristics of the study site. The site with clumped food distribution (OMYK) exhibited larger subgroups, as predicted by the ecological constraints model (ECM; Chapman et al. 1995). However, our results depart from ECM predictions since the site with higher food tree basal area (i.e., food patch density) (MABR) had smaller subgroups. According to the ECM, higher food availability for a given area leads to larger subgroups because of decreased travel costs and decreased competition for food (Chapman et al. 1995).

The increase in subgroup size with fruit availability in OMYK also supported the ECM, which states that larger food patches can give rise to larger subgroups (Janson 1988; Chapman et al. 1995). However, in MABR, the opposite occurred; subgroup size decreased with fruit availability, similar to findings made by Rimbach et al. (2014),

whose field site was, like MABR, a tropical rainforest with high annual rainfall (MABR: 2539 mm, this study; Hacienda San Juan del Carare: 3496 mm, Rimbach et al. 2014). We point to the importance of the environmental characteristics of the study sites. Annual rainfall in OMYK and other sites related to results supporting the ECM was lower and typical of seasonal tropical forests (OMYK: 1425 mm, this study; Santa Rosa National Park: 1527 mm, Chapman et al. 1995). In those sites, changes in subgroup size were positively related to fruit availability. Thus, the opposed variations in subgroup size with fruit availability between OMYK and MABR might be related, in part, to bioclimatic characteristics that were related to the forest, such as species diversity, phenology, or productivity. This might also explain why Korstjens et al. (2006) found that spider monkey subgroup size varied in a curvilinear fashion with rainfall across their range (it increased with rainfall up to 2500 mm and then slightly decreased).

The differences in the effects of the variance that was associated with food resources on subgroup size between sites also support the importance of characterizing particular habitat attributes. In MABR, subgroups tended to be larger (suggesting fewer consensus costs and greater cohesion) when the variance of fruiting trees increased, as proposed by Sueur et al. (2011), whereas in OMYK, subgroup size decreased with increasing variance of fruiting trees. However, at higher variance, subgroup size converged to a similar size (between three and four individuals, Figure 2.1b) in both study sites, while it diverged at low variance (and was larger in OMYK than in MABR). In both sites, high variance occurred when 20–100% of the trees from 30 to 50% of the food species were bearing fruit. The convergent values of subgroup size at greater values of variance are not far from what Korstjens et al. (2006) found as the median subgroup size (3.5, range 3–4.8) when considering different populations along the geographical distribution of *A. geoffroyi*. As Sibly (1983) had proposed, the cost-benefit dilemma associated with group size suggests that at least theoretically, there might be an optimal group size that maximizes individual fitness. Yet, according to Sibly (1983), this optimal group size tends to be unstable and larger than would be expected. The

divergent values of subgroup size at lower variance values suggest that this spatial variability in time influences subgroup size in different ways. These differences in subgroup size could be a result of contrasting local conditions of fruit availability, which interestingly result in similar variances of fruiting trees.

A low variance of fruiting trees could mean two opposite situations: that either almost none or almost all of the food trees were fruiting. For instance, we observed the lowest variance in OMYK when 10–50% of the trees of six of the top ten food species were bearing fruit (high fruit availability); in MABR, the lowest variance occurred when 35% of the trees of only one species (*Dialium guianense*) of the top eight food species were bearing fruit (low fruit availability). Therefore, low variance of fruiting trees in OMYK, where food trees are clumped, could promote consensus in decision-making for individuals aggregated in larger subgroups, more than at higher variance of fruiting trees; whereas in MABR, the site with a more homogeneous food distribution, individuals would incur in higher consensus costs, thereby promoting segregation at a low variance of fruiting trees.

2.7.2 Subgroup composition

The results for subgroup composition were contrary to our expectations for both study sites. Neither fruit availability nor the different characteristics of the sites influenced our index of subgroup composition, as happened with subgroup size. Chapman et al. (1995) found that the number of adult males in spider monkey subgroups changed with food density, but not with the number of adult females. Pinacho-Guendulain and Ramos-Fernández (2017) found a stronger association among females, but not among males nor between both sexes, when trees of *Brosimum*, one of the most important food species in OMYK, exhibited lower fruit availability. When fruits of this species were very abundant, subgroups tended to be mixed. Another reason why subgroup

composition did not change with the variables related to fruit resources, even when there was a slight tendency for female proportion to decrease when fruiting trees were more variable, and was similar between study sites, may be that subgroup composition depends more upon demographic and social factors than on fruit resources. According to Shimooka et al. (2008), changes in sex ratio could be due to the birth of individuals, mortality rates and migration. Social factors are a possible basis of female-male interactions (Aureli et al. 2008) that could influence the sexual composition in subgroups through time.

2.7.3 Fission rates

Our results for fission rates support predictions related to the ECM and to the scenarios proposed by Sueur et al. (2011) in OMYK, but not in MABR. As predicted by Sueur et al. (2011), subgroups tended to be more cohesive when rainfall increased in the seasonal site (OMYK), i.e., where variability is temporally predictable. This prediction was similar to what Smith et al. (2008) found with hyenas (*Crocuta crocuta*), where clans were more aggregated during periods of abundant prey. In MABR, our results would suggest that individuals experience difficulties in consensus decision-making when rainfall increased. It is likely that the uniform distribution of food trees, the larger food patches, and the stability of IFA through time (Figure S1) in MABR promoted dispersion of individuals. Compared to OMYK, MABR could be an example of low spatial variability or homogeneity, which would lead to a low FFD, according to the scenarios posed by Sueur et al. (2011). The opposite changes of fission rate with rainfall in both sites could also be due to other factors that were not measured in our study, for example, changes in foliage density that could impede or favor visual contact.

As suggested by Sueur et al. (2011), we observed that subgroups tended to be more unstable when there was high temporal variability in food resources (e.g., high

seasonality). In our case, very low or very high fruit availability could be comparable to the scenario of high temporal variability that was posited by Sueur et al. (2011). Further, a low variance of fruiting trees could represent this scenario because, as we previously mentioned, it occurs when either almost none or almost all of the food trees are fruiting. Under these conditions, individuals could face consensus costs and conflicts of interest, which would be manifested in higher fission rates. However, subgroups tended to be more stable with low fruit availability, regardless of the variance of fruiting trees. Therefore, fruit scarcity could promote cohesion and consensus decision-making when subgroup size is small, as stated by the ECM, for example, and particularly, in OMYK. Besides habitat characteristics, another factor influencing FFD could be demography. Lehmann and Boesch (2004) support the idea that demographic factors, such as group size, affect fission-fusion patterns. In their studies of chimpanzees, these authors found that small communities were more cohesive. They argue that group size may affect the social organization of chimpanzees by limiting absolute subgroup size and by reducing the need for flexibility.

Another important aspect to consider in behavioral studies that are related to FFD and the ECM is the use of different variables related to the quantity and distribution of food and its variability (e.g., food availability, patch size, temperature, rainfall, season). The fact that every variable can be measured in different ways can complicate the comparisons between studies. Moreover, it is important to be careful when making comparisons between sites; for instance, the variance of fruiting trees was used with the objective of measuring spatial variability during certain periods of the study, yet its meaning varied according to the site, even when it was measured equally on both sites.

Different locations within the range of a species with a wide with a wide distribution, such as *A. geoffroyi*, are accompanied by differences in climate and vegetation composition, structure, and phenology. This can give rise to the expression of behavioral plasticity, as it has often been observed (Korstjens et al. 2006; Kamilar and

Baden 2014). Thus, subgroup size and fission rates could depend not only upon food availability and its variability, but also on particular habitat contexts, such as food distribution and density. This suggests that FFD in spider monkeys involve a very flexible behavioral strategy that allows them to cope with a locally fluctuating environment and across their geographic range. Characteristics of OMYK might permit individuals to exist in larger subgroups, even more so during periods of high fruit availability, but on this site, smaller subgroups occur when trees are more variable in their fruiting. The opposite happened in MABR, where food availability was more stable temporally and distributed more evenly spatially, i.e., smaller subgroups when fruit availability increased and larger groups during periods of high variability in fruiting trees.

In conclusion, our case study captured intra-specific differences in FFD that were related to divergent responses as part of a behavioral strategy for coping with spatiotemporal fluctuations in food-resource availability. Our results suggest that changes in fruit availability and the characteristics of the habitat influence FFD in spider monkeys. Even when this case study presents data from only two sites, with strictly one group of spider monkeys in each site, the different results between the study sites suggest caution when making generalizations based on a single habitat or a short study period (which our study could not avoid). We therefore strongly encourage undertaking comparisons of longer-term studies in different habitats.

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CHAPTER 3

ENVIRONMENTAL AND SOCIAL FACTORS AFFECTING BEHAVIORAL SYNCHRONY IN SPIDER MONKEYS

3.1 Description of the article and contribution

Collective decisions and behavioral synchronization are part of life in groups and of FFD in spider monkeys. In this chapter we show how behavioral synchrony changes with the environment (i.e. fruit availability), and with social factors such as subgroup size and female ratio in subgroups; and sex composition in dyads. We also tested how behavioral synchrony is related to time of the day and spatial cohesion. Only a few studies in the literature about FFD have incorporated behavioral synchrony except those about segregation. Besides, behavioral synchrony has been studied mostly in herbivores with high sexual dimorphism. This is one of the few studies on behavioral synchrony with a frugivorous species and species with a relatively weak sexual dimorphism.

In this chapter, I contributed with the idea, and the hypotheses were better defined with the help of Gabriel Ramos-Fernández, Sophie Calmé and Ellen Andresen. For this chapter, I also used data from MABR and OMYK. As in the previous chapter, I collected the data in MABR with the help of Rafael Lombera, Isidro Lopez Lira, Violeta González Alcaraz, and many students. The data from the long-term project at OMYK were provided by Gabriel Ramos-Fernández, Filippo Aureli, Colleen Schaffner, and Laura Vick. I organized the data bases corresponding to both objectives. I ran the statistical analyses with the help of François Rousseu, who introduced me to additive general models. Sophie Calmé, Gabriel Ramos-Fernández and Ellen Andresen made

substantial revisions to the chapter and I discussed with them several flaws. We expect to submit this chapter to the journal *Animal Behaviour*.

Environmental and social factors affecting behavioral synchrony in spider monkeys

Adriana R. Aguilar Melo, Gabriel Ramos-Fernández, Ellen Andresen, Sophie Calmé

3.2 Abstract

Behavioral synchrony helps to maintain the benefits of living in group. In this study we explore the relationship between fission-fusion dynamics (FFD) and behavioral synchrony in spider monkeys (*Ateles geoffroyi*), a sex-segregated species with a high degree of FFD. We aimed to explore how the environment (i.e. food availability), subgroup characteristics (i.e. size, sexual composition), spatial cohesion and time of day, influence behavioral synchronization in subgroups and dyads. To address this objective we split it in two parts: (i) behavioral synchrony related to environmental, social, and internal factors, and (ii) behavioral synchrony associated with spatial cohesion. At the subgroup level, we obtained information from two groups of spider monkeys in Chiapas, Mexico, while at the dyadic level information came from one group in the Yucatan Peninsula, Mexico. At the subgroup level, overall synchrony (all activities pooled together) and feeding synchrony decreased with subgroup size. Also feeding synchrony was lower in subgroups with mixed composition while the opposite occurred for resting synchrony. Feeding synchrony increased with fruit availability in one of the groups and decreased in the other, while traveling synchrony increased with fruit availability in both groups. Feeding synchrony was higher at the beginning and at the end of the day, while resting synchrony was higher only at the end of the day, and

traveling synchrony at the beginning of the day. At the dyadic level, we found that behavioral synchrony increased with spatial cohesion, and dyads of the same sex were more synchronized. Synchrony in male-male dyads changed less with fruit availability than in the other dyads, but changed more with the inter-individual distances than in the other dyads. We discuss the possible drivers of behavioral synchrony in the FFD of a frugivorous primate species, and conclude that scramble competition, social preference among sex-classes, and spatial cohesion are likely the stronger drivers explaining variation in group behavioral synchrony.

Keywords: Collective behavior, coordination, fruit availability, subgroup composition, spatial cohesion.

3.3 Introduction

Behavioral synchronization occurs when individuals in a group perform the same activity at the same time (King and Cowlishaw, 2009). Synchrony in groups helps social species to increase the benefits and minimize the costs of living in groups (King and Sueur, 2011), like finding food and avoiding predation (Ruckstuhl and Neuhaus, 2001; Pays et al., 2007; King and Cowlishaw, 2009). Consensus and collective decisions are required to achieve this state of activity coordination (Dostalkova and Spinka, 2007), that leads to group stability (Conradt and Roper, 2000). However, consensus decisions can be costly because synchronization requires that individual group members compromise their own activity budgets in order to match the behavior of their group mates (Conradt and Roper, 2000; Conradt and List, 2009). Consecuently, when differences between individuals in the group lead to dissimilar decision options, conflicts of interest occur (Conradt and List, 2009), and behavioral synchrony can be difficult (Conradt and Roper, 2000; Ruckstuhl and Kokko, 2002).

Behavioral synchronization can be modulated by (1) uncertainty in the environment (Conradt and List, 2009; Sueur *et al*., 2011), (2) group size and spatial cohesion among individuals (Calhim *et al*., 2006; King and Sueur, 2011), (3) individual differences in energy needs (Sueur *et al*. 2011), and (4) by the time of the day (Michelena *et al*., 2006, Patzelt *et al*. 2006). Uncertainty in the environment refers to factors, such as the spatial and temporal predictability of food resources, which can eventually cause conflicts of interest and group instability (Bourgoin *et al*., 2018; King and Cowlishaw, 2009). Sueur *et al*. (2011) hypothesize that consensus decisions and stability are expected when all the food patches contain resources of similar quality and quantity, but also if it becomes difficult to foresee their temporal availability. However, when food patches differ widely in quality and quantity of resources, conflicts of interest between individuals with different requirements increase as well as consensus costs (Sueur *et al*. 2011).

Regarding group size, this variable can have an impact on behavioral synchrony because of the difficulty of being organized (Calhim *et al*., 2006) or because foraging competition can increase leading some individuals to engage in other activities (Calhim *et al*., 2006; King and Sueur, 2011). For instance, benefits of collective vigilance in kangaroos (*Macropus giganteus*) increases up to seven individuals and decreases thereafter with each additional member (Pays *et al*., 2007). Groups can become so large that no group member has a global overview of the entire group, affecting the transmission of information and therefore, group coordination (Conradt and List, 2009; King and Sueur, 2011). Thus, group size can also be related to the degree of spatial cohesiveness, which in turn can affect group coordination. For example, individuals of Japanese macaque (*Macaca fuscata*) staying close to each other are more likely to take the same travel route and visit the same food patches (Sugiura *et al*. 2011). Likewise, King and Cowlishaw (2009) found that when cohesion was higher, synchrony increased in Chacma baboons (*Papio ursinus*). Spatial cohesiveness can facilitate behavioral synchrony by visual communication (Deneubourg and Goss, 1989), information exchange or simply by reacting to the action of others (Dostálková and

Špinka, 2007) using social cues (e.g. feeding, fleeing and mating; Dall *et al*., 2005). The degree of spatial cohesiveness can vary not only according to group size (Conradt and List, 2009; King and Sueur, 2011; Pays *et al*., 2007), but also according to group activity, seasonality, and affiliative social behavior (Sugiura *et al*., 2011).

In terms of individual differences in energy needs, behavioral synchrony can be affected by differences in body mass, reproductive status and nutritional requirements, which in the case of social animals can be pronounced, especially between the sexes (Ruckstuhl and Neuhaus, 2000). Several authors have proposed that the distribution of synchrony costs between group members depends on how homogenous members are with respect to their optimal time budgets (Conradt and Roper, 2000; Ruckstuhl and Kokko, 2002). According to this idea, differences in optimal time budget are often associated with different nutritional requirements between members with different body mass and reproductive status (activity budget hypothesis; Ruckstuhl and Neuhaus, 2000; Michelena *et al*., 2006, Bourgoin *et al*., 2018). In addition, internal factors such as the level of satiety (Michelena *et al*., 2006) or energetic requirements (Macleod et al., 2005, Patzelt *et al*., 2011), may also trigger activity timing and consequently synchrony. So, synchronization could be facilitated if individuals forage intensively at the start of the day to gain energy. For instance, baboons (*Papio papio*) presented a higher feeding synchronization in the morning than in the afternoon (Patzelt *et al*., 2011). Baboons spend time foraging in few and large subgroups before leaving their sleeping trees, while in the afternoon, smaller distinct subgroups return to the sleeping trees (Patzelt *et al*., 2011). This suggests that individual energy and hunger levels can become more variable as the day progresses, due to differences in foraging success and satiation requirements (Michelena *et al*., 2006).

All the factors mentioned previously, such as energy requirements, other sex-related differences, group size, and spatial cohesion can interact together and with the environment to constrain behavioral synchrony and cause group instability. For

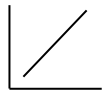
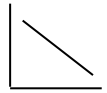
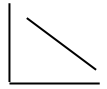
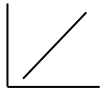
instance, Calhim *et al*. (2006) showed that behavioral synchrony varied with sex and group size in feral goats (*Capra hircus*). King and Cowlishaw (2009) found that synchrony increased with the number of pregnant females, while it decreased with the number of sexually swollen females in groups of Chacma baboons. In the same study, synchrony also decreased through the day, but it was higher in woodland than in desert (King and Cowlishaw, 2009).

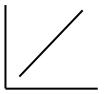
Individuals that have important differences in activity budgets and therefore are unable to synchronize may be segregated from the group (Ruckstuhl and Kokko, 2002), as occurs in groups with high fission-fusion dynamics (FFD; Sueur *et al*., 2011). FFD refers to the temporal variation in subgroup size, composition and spatial cohesion that occurs in different animal groups including primates, ungulates and bats (Aureli *et al*., 2008). The degree of spatial and temporal cohesion of group members in animals with FFD varies both within and across taxa (Aureli *et al*., 2008). Behavioral synchrony has been well studied in ungulates (Pays *et al*., 2007), but more studies are needed for a broad range of mammal species (Ruckstuhl and Neuhaus, 2002). In particular, there are only a few studies on frugivorous mammals, most of which address collective movements but rarely synchronization (e.g., Meunier *et al*., 2006; King and Sueur, 2011), even when fruit availability fluctuates naturally, and sex segregation is common in these species. Furthermore, variability in subgroup size, composition and cohesion, as occurs in FFD, has been rarely integrated into studies on behavioral synchrony (e.g., King and Sueur, 2011). One can postulate that FFD is a lack of behavioral synchrony between certain members of a group due to variation in the benefits and costs of subgroup caused by the environment, subgroup size, and differences between members.

In this study, we explore how behavioral synchrony varies in the FFD of spider monkeys (*Ateles geoffroyi*). Our first objective was to determine the influence of environmental, social, and time of the day (as an internal factor related to energy requirements) on behavioral synchrony (in general, and specifically for feeding, resting and traveling) in

groups of spider monkeys. Our hypothesis was that changes in behavioral synchrony are related to environmental factors (fruit availability; Smith *et al*., 2008; Sueur *et al*., 2011), social factors (subgroup size and proportion of females; Sueur *et al*., 2011), and internal factors (time of the day; Michelena *et al*., 2006; see associated predictions in Table 3.1). Our second objective was to test the influence of fruit availability, sexual composition and spatial cohesion on dyadic behavioral synchrony in spider monkey. We hypothesized that behavioral synchrony in dyads is related to fruit availability and sexual composition because of possible conflicts of interest through foraging competition (Smith *et al*., 2008, Sueur *et al*., 2011) due to sexual differences in activity budgets, diet, and social preferences (Conradt and Roper, 2003; Ruckstuhl and Neuhaus, 2000, Bourgoin *et al*., 2018; see predictions in Table 3.2). Finally, we hypothesized that high spatial cohesiveness influences dyadic behavioral synchrony (Dostálková and Špinka, 2007; Conradt and List, 2009; Sugiura *et al*., 2011; see predictions in Table 3.2).

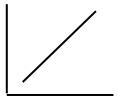
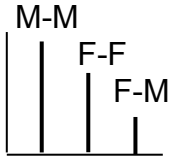
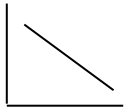
Table 3.1. Predictions for the relationships between behavioral synchrony in spider monkeys and environmental, social and time of the day.

Independent variable	Prediction		Source
Environmental: fruit availability	P1: S, FS and RS will increase with fruit availability (IFA) because of a reduction of foraging competition, fewer conflicts of interest among group members, and higher consensus		Smith *et al*., 2008, Sueur *et al*., 2011
	P2: TS will increase when IFA decreases because of an increase in foraging competition and more conflicts of interest among group members impeding consensus		
Social: subgroup size	P3: S, FS, and RS will decrease with increasing subgroup size because of a higher probability of foraging competition, and a higher difficulty in maintaining coordination		Calhim *et al*., 2006; King and Sueur, 2011; Sueur *et al*., 2011
	P4: TS will increase with subgroup size because of a higher probability of foraging competition, and therefore higher difficulty in maintaining coordination		
Social: female proportion (0-1)	P5: S, FS, and RS will decrease in mixed subgroups (female proportion = 0.5) due to differences between sexes (e.g. diet requirement), and will increase in homogeneous subgroups (female proportion = 0 or 1)		Conradt, 1998; Hartwell *et al*., 2014; Symington, 1988; Wallace, 2008
	P6: TS will increase in mixed subgroup composition (female proportion = 0.5) due to the differences between sexes (e.g. diet requirement), and will decrease in homogeneous subgroups (female proportion = 0 or 1)		

Independent variable	Prediction		Source
Internal: effect of time of the day on metabolism	P7: S and FS will be higher at the beginning of the day in response to internal factors (energetic needs).		Michelena *et al*., 2006, Patzelt, 2011
	P8: RS will increase during the day in response to internal factors (satiation). TS will not change importantly with time of the day as this activity relates to different activities with different purposes (searching food patches, sleeping sites, or patrolling).		
Socio-environmental: Groups A and B	P9: Behavioral synchrony will change differently according to the previous factors between the studied groups that present differences in fruit productivity, subgroup size and proportion of females.	N/A	Conradt, 1998; Calhim *et al*., 2006; Smith *et al*., 2008, Sueur *et al*., 2011 ; Hartwell *et al*., 2014

* Synchrony for all activities = S, Feeding synchrony = FS, Resting synchrony = RS, and Traveling synchrony = TS)

Table 3.2. Predictions for the relationships between dyadic synchrony in spider monkeys and spatial cohesiveness, as well as environmental (fruit availability) and social (dyadic sexual composition) variables.

Independent variable	Prediction		Source
Environmental: fruit availability	Dyadic synchrony will increase with fruit availability because higher resource abundance reduces foraging competition and conflicts of interest.		Smith *et al*., 2008; Sueur *et al*., 2011
Social: subgroup composition (M-M, F-F, M-F)	Dyadic synchrony will depend on the sexual composition of dyads. Male-male dyads will present higher level of synchrony than female-female dyads (due to different reproductive states among females) and female-male dyads (due to sex differences in activity budgets and diet, and to social preferences).		Conradt and Roper, 2003; Ruckstuhl and Neuhaus, 2000; Bourgoin *et al*., 2018
Spatial cohesiveness: inter-individual distances, IID	Dyadic synchrony will increase with higher spatial cohesiveness (smaller IID) because of improved transmission of information through visual communication and because individuals could be in the same place for the same reason.		Dostálková and Špinka 2007; Conradt and List, 2009; Sugiura *et al*., 2010

* M-M = male-male dyad; F-F = female-female dyad; M-F = male-female dyad; IID = Inter-individual distances.

3.4 Methods

3.4.1 Study species

Spider monkeys present a high degree of fission-fusion dynamics, meaning that spatial cohesion and individual membership vary largely in a group over time (Aureli *et al*., 2008). This species is not highly sexually dimorphic but tends to present sexual segregation (Ramos-Fernández *et al*., 2009, Hartwell *et al*., 2014). Females are considered the less social sex (Aureli and Schaffner, 2008), and they range over smaller areas, spending less time traveling and more time feeding and resting than males (Symington, 1988; Hartwell *et al*., 2014).

3.4.2 Study sites

We carried out fieldwork in two study sites. Data for the first objective (group behavioral synchrony related to environmental, social and internal factors) were obtained in the Montes Azules Biosphere Reserve (MABR; 16°05′58″ N, 90°52′36″ W, 10-50 m a.s.l.) in the state of Chiapas. The mean annual temperature in MABR is 24.0 °C, and mean annual rainfall is 2881 mm (SEMARNAP, 2000). Vegetation is mainly tropical evergreen forest (SEMARNAP, 2000). Data for the second objective (dyad behavioral synchrony related to environmental and social factors, and to spatial cohesion) were collected 610 km north of MABR, in the protected area of *Otoch Ma´ax Yetel Kooh* (OMYK; 20°38′ N, 87°38′ W, 14 m elevation) in the Yucatan Peninsula. Mean annual temperature in OMYK is 24.3 °C, and mean annual rainfall is 1120 mm (1951-2010; Servicio Meteorológico Nacional, 2015). OMYK is dominated by different successional stages of seasonal tropical forest (García-Frapolli *et al*., 2007).

3.4.3 Study groups and activity sampling

In MABR we studied two groups of spider monkeys (hereafter group A and group B) over one year (May 2014- April 2015), while in OMYK we studied one group over two years (January 2013 – December 2014). Each group in MABR had its own territory, i.e., home ranges did not overlap and were separated by 5 km approximately. During our study, group A consisted of 22 individuals (8 adult and sub-adult females, 8 adult and sub-adult males, and 6 young), and group B consisted of 25 individuals (10 adult and sub-adult females, 8 adult and sub-adult males, and 7 young). Group A and B present differences in subgroup size and proportion of females and in the availability of fruits in their respective home ranges (Table S1). For each group, observation periods lasted 6-8 d per month from May to December 2014, and 14 d per month from January to April 2015. In OMYK the group included 38 individuals (15 adult and sub-adult females, 7 adult and sub-adult males, and 16 young) in 2013; and 47 individuals (20 adult and sub-adult females, 9 adult and sub-adult males, and 18 young) in 2014. In OMYK, observation periods lasted 14 d per month, from January 2013 to December 2014. Groups in OMYK have been monitored since 1997 and groups in MABR have been the object of several independent research projects since 1998 resulting in habituation to humans.

Subgroups in both study sites were followed 4-8 h per day between dawn and dusk, during which we performed instantaneous scans every 20 min (Martin and Bateson, 2007). We defined a subgroup as all individuals observed within a distance of ≤ 30 m from at least one other subgroup member (Ramos-Fernández, 2005). The subgroup we followed depended on the focal individual we chose at the beginning of every sampling day. Data collection in MABR totaled 941 instantaneous scan samples over 314 h of observation for Group A, and 804 instantaneous scan samples over 268 h for

Group B. Instantaneous scan samples and observation times in OMYK totaled 2150 scan samples and 716 h in 2013; and 2665 scan samples and 888 h in 2014.

In OMYK we used dyads as the social scale to measure behavioral synchrony. We considered dyads of individuals simultaneously present in the same subgroup in a given instantaneous scan sample. For each scan sample in OMYK, and according to our definition of subgroup, we recorded the inter-individual distances (IID) between all subgroup members (identified by facial marks and other unique features). Inter-individual distances (IID) were estimated visually by field assistants who received previous training. IID were consistent between observers (Kendall's coefficient of concordance; $w = 0.38$, $p < 0.001$), while real and estimated distances, evaluated using a Pearson-product moment correlation were also consistent ($r = 0.95$, $p < 0.05$). Using individual identity, we obtained the IID by dyad, and then classified them by sex obtaining three classes: (1) female-female (F-F), (2) male-male (M-M), and (3) male-female (M-F).

For each scan sample, we recorded the time, subgroup size and composition. Sexual composition was obtained through the proportion of females in a given subgroup (adult and sub-adult females/subgroup size; Ramos-Fernández and Morales, 2014). We also recorded the activities carried out by the individuals in the subgroup. We considered the following activity categories: (1) *Feeding*, which included short movements (≤ 3 s) to acquire food, manual and oral manipulation of food items, and longer movements (> 3 s) associated with food searching within a tree or an abutting branch of a nearby tree; (2) *Traveling*, i.e., longer distance movements (≥ 25 m); (3) *Resting*, i.e., when individuals were stationary or passive; (4) *Social interactions*, which included activities such as plays, grooming, embraces, chases, aggressions and copulations, between two or more individuals; (5) *Others*, which included behaviors like drinking water, vigilance, vocalizations, and moving briefly (< 3 s) for any purpose but feeding. For all analyses we considered only adult and sub-adult individuals.

With this information, we calculated for each scan the following response variables: 1) *Synchrony for all activities* (S, individuals doing the same activity/total number of individuals); 2) *Feeding synchrony* (FS, individuals feeding/total number of individuals); 3) *Traveling synchrony* (TS, individuals traveling/total number of individuals); 4) *Resting synchrony* (RS, individuals resting/total number of individuals); and 5) *Social interactions synchrony* (individuals in social interactions/total number of individuals). We analyzed the synchrony for all activities, but as each activity has different adaptive functions and therefore they could react differently to the independent variables, we decided to analyze each activity synchrony separately. For each scan sample in OMYK we noted if both individuals in every dyad were doing the same activity or not. With this information, *Synchrony for all activities* (S) provided two responses: synchronized (1) or not synchronized (0).

3.4.4 Index of fruit availability

We assessed fruit availability along 3-m wide phenological trails running through the study groups' ranges. In MABR, the phenological trail was ca. 2.5 km-long for group A, and ca. 2 km long for group B. In OMYK, the phenological trail was ca. 2 km long. Phenological trails were monitored after every observation period for each group in MABR and every second week in OMYK; we registered the presence/absence of fruit on 10 individuals of each of the top fruit species for spider monkeys. In MABR the top fruit species were the 8 most important species in the spider monkeys' diet in continuous forest at the study site, according to records of their monthly diet in 2007 and 2008 (Chaves *et al*., 2012). In OMYK the top fruit species were the 10 most important food species for spider monkeys according to monthly records of their diet between 1997 and 2004 (Pinacho-Guendulain and Ramos-Fernández, 2017; Aguilar-Melo *et al*., 2018). An index of fruit availability (IFA) was calculated as the sum of the proportion of trees bearing fruits for all the monitored species in the corresponding

phenological trail per observation period, multiplied by their density (individuals/ha) and the sum of the DBH per ha for each species (Smith-Aguilar *et al*., 2016).

3.4.5 Data analyses

Before running the models, we assessed collinearity between the independent variables (evaluating the Variance Inflation Factors) and found none. We also tested for temporal autocorrelation among sampling days by extracting residuals from the complete model and calculating the absolute difference between each pair of residuals within each group/year/date block. We then classified time differences in equal intervals and plotted the variance of residual differences in each interval against the median time value for each interval. The relationship was flat, suggesting that there was no temporal autocorrelation.

For the first objective (Behavioral synchrony related to environmental, social, and internal factors), we used generalized additive models (GAMs) to assess the relationships between the response variables and explanatory variables (Table 3.3). In GAMs, the linear predictor is specified as a sum of smooth functions of some or all the covariates (Wood, 2004). As we incorporated the time of day in our models, we thought that the utilization of GAMs was pertinent, because they permit to analyze models with temporal autocorrelation (Wood, 2004). GAMs also permit to handle data with error distributions departing from normality, such as presence/absence data with a binomial error distribution (Leathwick, 1998). In this case, we did not run the analyses for the *Social interactions synchrony* because this behavior occurred in only 3.9% of the scans; neither did we run the analyses for *Other behaviors* because of the diversity of activities in this category. We fitted a binomial distribution with the logit-link function for all response variables. We included all possible two-way interactions between explanatory variables.

We fitted the models using the 'mgcv' package (Wood, 2011). To find the most parsimonious models, we began with the saturated model (Table 3.3), and then used backward elimination through ML smoothness selection criterion to sequentially remove the variables with the highest P-values (Wood, 2018), using a threshold of $\alpha = 0.05$ to keep variables. The gam function in the mgcv package does not provide the output of the cross-validation in terms of λ, but uses a term called the effective degrees of freedom (edf, from 0 to infinity), which is a sort of mathematical transformation of λ (Kleinbaum, 2005). The higher the edf, the more non-linear the smoothing spline (Kleinbaum, 2005). The resulting models were described by plotting both the inference and the smooth series of GAM for the significant effects between the dependent and the explanatory variables.

For the second objective (Behavioral synchrony and spatial cohesion) we used generalized linear mixed-effects models to test the relationship between Dyadic synchrony and explanatory variables (Table 3.3). We included the identification of the dyad members as a random effect. We fitted the models using the lme4 package (Bates et al., 2015). We performed all the analyses in R version 3.5.2 (R Core Team, 2018). For the models of both objectives, we began with the saturated models (Table 3.3) and then we used backward elimination to remove the variable with the highest *P*-value according to criterion $\alpha = 0.05$ (Bolker, 2007).

Table 3.3. Saturated models to assess the relationships between behavioral synchrony and environmental and social factors in MABR, and to test the relationship between behavioral synchrony and spatial cohesion in OMYK.

Response variable	Model
Behavioral synchrony related to environmental, social, and internal factors	
Synchrony for all activities	~ Group + Subgroup size + Female proportion + IFA + Subgroup size × Group + Female proportion ×Group + IFA × Group + Subgroup size × Female proportion^2 + Subgroup size × IFA + s(time, by = Group) + Female proportion × IFA
Feeding synchrony	
Traveling synchrony	
Resting synchrony	
Behavioral synchrony and spatial cohesion	
All activities synchrony	~ IID + dyad composition + IFA + IFA× dyad composition + IID × dyad composition

* s refers to the smoothing function used in GAMs to define the influence of factors.

3.5 Results

3.5.1 Behavioral synchrony related to environmental, social, and internal factors

In synchrony for all activities, the most parsimonious model described 8.6% of the deviance. The models for the synchrony in particular activities explained between 10.7% (for traveling synchrony) and 16.5% (for feeding) of the variations in each evaluated activity (see Table B2). Groups A and B presented some differences in the

way fruit availability, sub-group size, female proportion and time of day influenced behavioral synchrony (synchrony for all activities, feeding synchrony, traveling synchrony and resting synchrony; Tables 3.4, 3.5, 3.6 and 3.7).

Table 3.4. Mean proportion of individuals in a subgroup carrying out in synchrony an evaluated activity.

Activity	Proportion of individuals			Comparison between A and B	
	Both groups	Group A	Group B	Z	p
Resting	0.40	0.36	0.45	207560	*< 0.001*
Traveling	0.28	0.28	0.27	233280	0.509
Feeding	0.18	0.20	0.16	245460	*0.003*
Other	0.12	0.14	0.10	245810	*< 0.001*
Social interactions	0.02	0.02	0.03	229060	0.898

Synchrony for all activities was affected by IFA, subgroup size and time. The effects of subgroup size and time were different between groups A and B (Table 3.5). Broadly, synchrony for all activities increased as expected in both groups with fruit availability (Figure 3.1a). In both groups, synchrony for all activities decreased as expected when subgroup size increased but group B decreased in a more pronounced way (Figure 3.1b). Finally, synchrony for all activities was relatively constant during the day in group A (Figure 3.1c) but it tended to increase slightly in group B (Table 3.5).

All the factors influenced feeding synchrony, and in some cases group A and group B presented some differences (Table 3.6). For instance, the proportion of individuals

feeding at the same time increased with the increase of fruit availability in group A but it decreased in group B (Table 3.6, Figure 3.2a). As expected, feeding synchrony decreased with subgroup size in both groups, but with a stronger effect in group B (Table 3.6, Figure 3.2b). Feeding synchrony was also affected differently by female proportion in both groups. In group A, feeding synchronization was slightly higher when subgroups were more homogeneous (mostly males or mostly females, Table 3.6, Figure 2c), while in group B, feeding synchrony steadily decreased when the proportion of females increased. Feeding synchrony changed as expected with the time of the day in both groups with a slight difference around 10 am (Table 3.6, Figure 3.2d), but in general both groups presented a higher feeding synchrony in the morning and at the end of the day (Figure 3.2d).

Traveling synchrony also responded to all the variables examined, with subgroup size being the most important (Table 3.7). Traveling synchrony also showed differences between groups (Table 3.7, Figures 3.2). In both groups, the proportion of individuals traveling at the same time increased with fruit availability, but this tendency was more pronounced for group B (Table 3.7, Figure 3.2e). In relation with subgroup size, traveling synchrony increased barely in group A and strongly in group B (Figure 3.2f). Traveling synchrony remained relatively stable with the time of day in group A and decreased in group B. Traveling synchrony was affected by the interaction between subgroup size and fruit availability (Figure 3.3ab). It increased with subgroup size when IFA values were low (around 4510) and decreased when subgroup size increased at the higher IFA values (around 11563). Traveling synchrony also increased with subgroup size when subgroups tended to be composed mostly by males; while decreased with subgroup size when subgroups were mostly composed by females (Figure 3.3b).

Resting synchrony responded mainly to subgroup size, female proportion and time of day (Table 3.8). There were also some differences between groups (Figure 3.2j-i, Table

3.8). Resting synchrony increased in group A and decreased in group B when subgroup size increased (Figure 3.2h). Resting synchrony was higher when subgroups had similar proportions of males and females; but this quadratic effect was more pronounced in group A (Figure 3.2i).

Table 3.5. Parameters and approximate significance of smooth terms in the best model explaining all activities synchrony of spider monkeys in MABR.

Explanatory variable	Estimate	SE	*Z*	*P*
(Intercept)	1.307	0.271	4.825	0.000
IFA	**0.000**	**0.000**	**2.543**	**0.011**
Group (B)	**1.116**	**0.342**	**3.265**	**0.001**
Subgroup size	**-0.122**	**0.05**	**-2.465**	**0.014**
Female proportion	-0.019	0.215	-0.862	0.389
Group: Subgroup size	**-0.27**	**0.095**	**-2.845**	**0.004**

	Edf	Ref.df	X^2	*P*
s(Time of the day)	**0.747**	**9**	**0.683**	**0.020**
s(Time of the day):Group A	3.111	9	2.803	0.172
s(Time of the day):Group B	**1.326**	**9**	**2.108**	**0.019**

* Best model: All activities synchrony ~ IFA × Group + Subgroup size + Female proportion + Time of day + Group × subgroup size + Time of day × group. Nubers in bold indicate variables with a significant effect. edf = effective degrees of freedom, s = the smooth factor.

Table 3.6. Parameters and approximate significance of smooth terms in the best model explaining feeding synchrony of spider monkeys in MABR.

Explanatory variable	Estimate	SE	*Z*	*P*
(Intercept)	-1.35	0.21	-6.42	0.000
IFA	**0.000**	**0.000**	**3.928**	**0.000**
Group	**1.599**	**0.344**	**4.653**	**0.000**
Subgroup size	**-0.136**	**0.034**	**-4.035**	**0.000**
Female proportion	**-2.117**	**0.512**	**-4.132**	**0.000**
Group B x IFA	**0.000**	**0.000**	**-4.629**	**0.000**
Group x Subgroup size	**-0.211**	**0.074**	**-2.835**	**0.005**
Group A x Female proportion	**2.328**	**0.455**	**5.115**	**0.000**
Group B x Female proportion	**1.561**	**0.485**	**3.216**	**0.001**

	Edf	Ref.df	X^2	*P*
s(Time of day)	**7.732**	**9**	**51.650**	**0.000**
s(Time of day):Group A	**4.107**	**9**	**18.150**	**0.000**
s(Time of day):Group B	**0.012**	**0**	**0.010**	**0.039**

* Best model: Feeding synchrony ~ IFA + Group + Subgroup size + Female proportion + Time of day + Group × IFA + Group × subgroup size + Group × Female proportion + Group × Time of day. Bold characters indicate variables with a significant effect.

Table 3.7. Parameters and approximate significance of smooth terms in the best model explaining traveling synchrony of spider monkeys in MABR.

Explanatory variable	Estimate	SE	*Z*	*P*
(Intercept)	-1.812	0.244	-7.437	0.000
IFA	**0.000**	**0.000**	**3.43**	**0.001**
Group (B)	**-1.899**	**0.275**	**-6.899**	**0.000**
Subgroup size	**0.229**	**0.046**	**5.01**	**0.000**
Female proportion	0.279	0.242	1.153	0.249
Group B x IFA	**0.000**	**0.000**	**3.023**	**0.003**
Group x Subgroup size	**0.386**	**0.057**	**6.716**	**0.000**
Subgroup size x IFA	**0.000**	**0.000**	**-3.556**	**0.000**
Subgroup size x Female proportion	**-0.125**	**0.059**	**-2.126**	**0.033**

	edf	Ref.df	X^2	*P*
s(Time of day)	0.016	9	0.015	0.234
s(Time of the day):Group A	**5.344**	**9**	**28.112**	**0.000**
s(Time of the day):Group B	**0.889**	**9**	**7.886**	**0.002**

* Best model: Traveling synchrony ~ IFA + Group + Subgroup size + Female proportion + Time of day + Group × IFA + Group × subgroup size + Subgroup size × IFA + Subgroup size × Female proportion + Group × Time of the day. Bold characters indicate variables with a significant effect.

Table 3.8. Parameters and approximate significance of smooth terms in the best model explaining resting synchrony of spider monkeys in MABR.

Explanatory variable	Estimate	SE	*Z*	*P*
(Intercept)	-0.966	0.159	-6.064	0.000
IFA	**0.000**	**0.000**	**-2.136**	**0.033**
Group (B)	**0.988**	**0.186**	**5.31**	**0.000**
Subgroup size	**0.094**	**0.029**	**4.096**	**0.000**
Female proportion	**2.263**	**0.423**	**5.345**	**0.000**
Group x Subgroup size	**-0.294**	**0.037**	**-7.966**	**0.000**
Group A x Female proportion	**-2.283**	**0.363**	**-6.29**	**0.000**
Group B x Female proportion	**-1.955**	**0.378**	**-5.174**	**0.000**

	edf	Ref.df	X^2	*P*
s(Time of day)	3.648	9	119.514	**0.000**
s(Time of the day):Group A	0.000	9	0.000	0.616
s(Time of the day):Group B	0.002	9	0.001	0.638

* Best model: Resting synchrony ~ IFA × Group + Subgroup size + Female proportion + Time of day + Group × Subgroup size + Group × Female proportion + Group × Time of the day. Bold characters indicate variables with a significant effect.

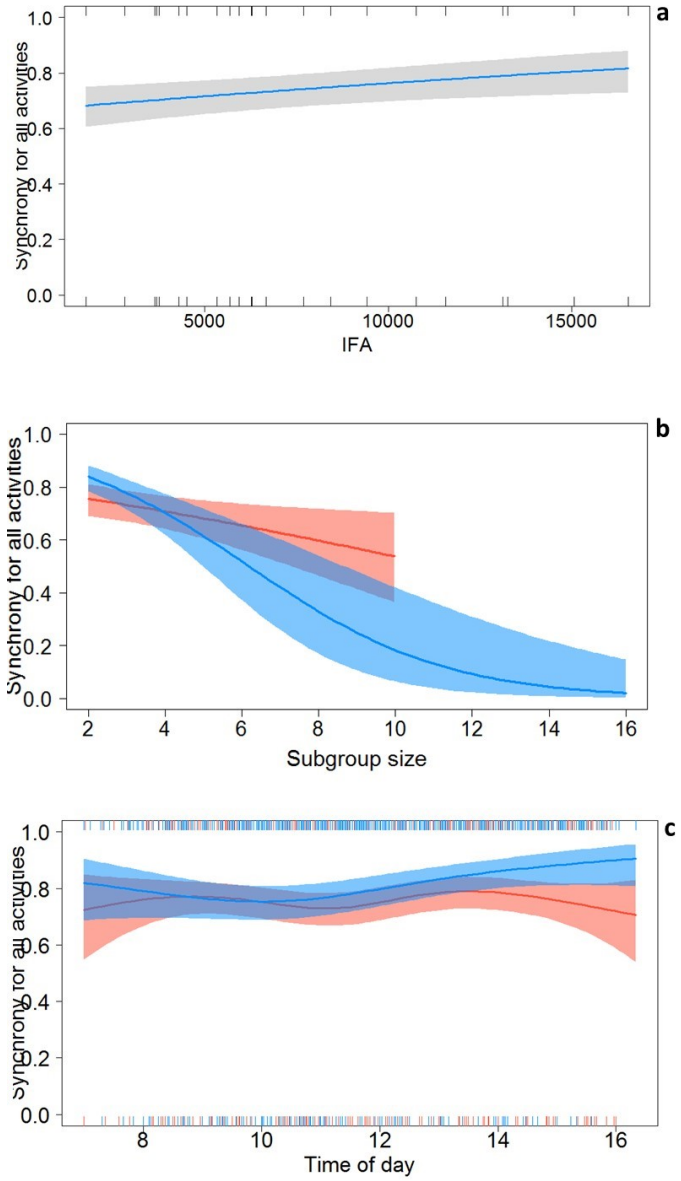


Figure 3.1. Parameters and fitted smoothed functions of all activities synchrony in response to a) Fruit availability (IFA), b) Subgroup size, and c) Time of the day, for both groups (gray), for group A (pink) and in group B (blue).

Shaded regions represent the approximate 95% pointwise confidence intervals.

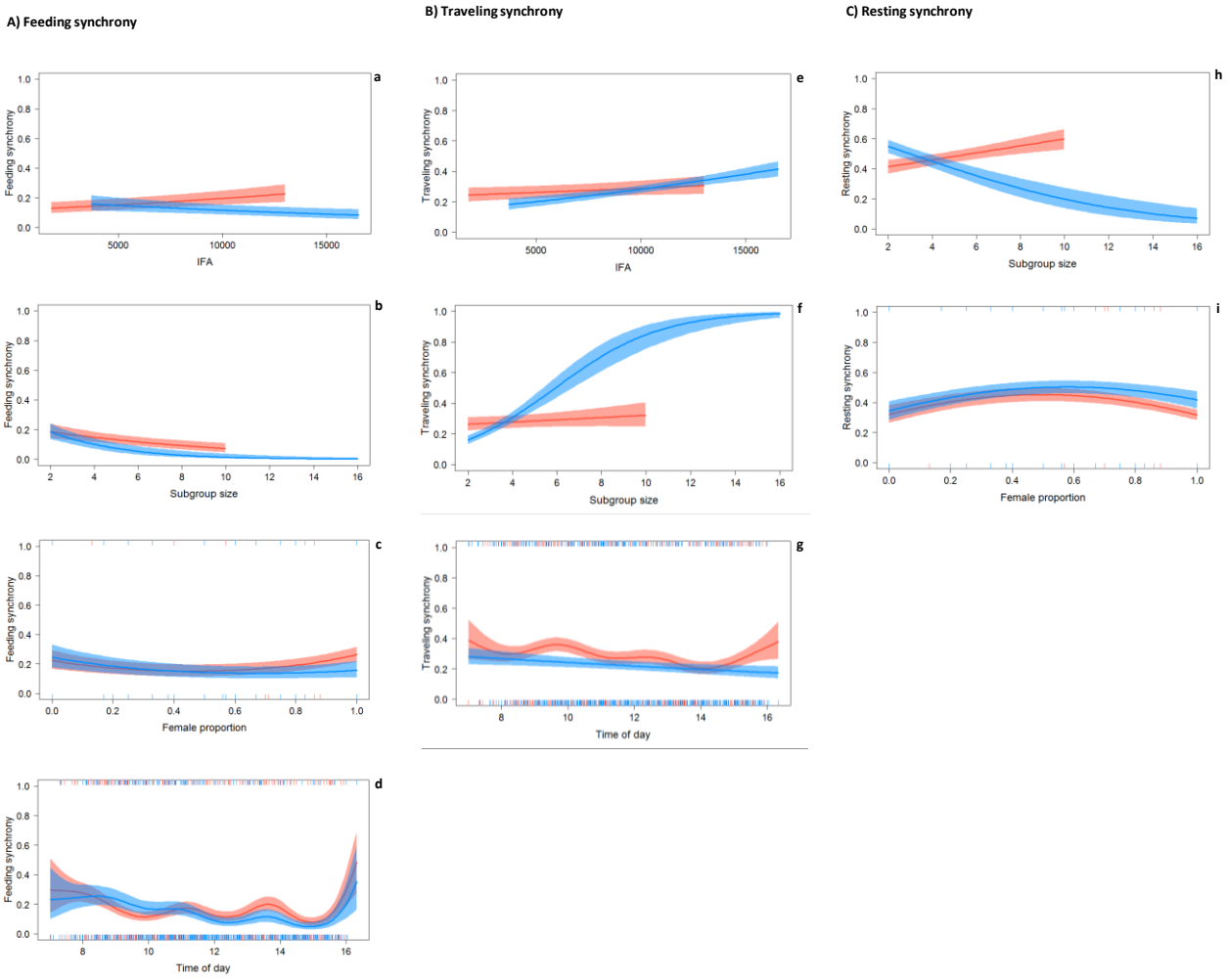


Figure 3.2. Parameters and fitted smoothed functions for feeding synchrony (a to d), traveling synchrony (e to g), and resting synchrony (h to i) in relation to fruit availability (IFA), subgroup size, female proportion and time of day, for group A (pink) and B (blue).

Shaded regions represent the approximate 95% pointwise confidence intervals.

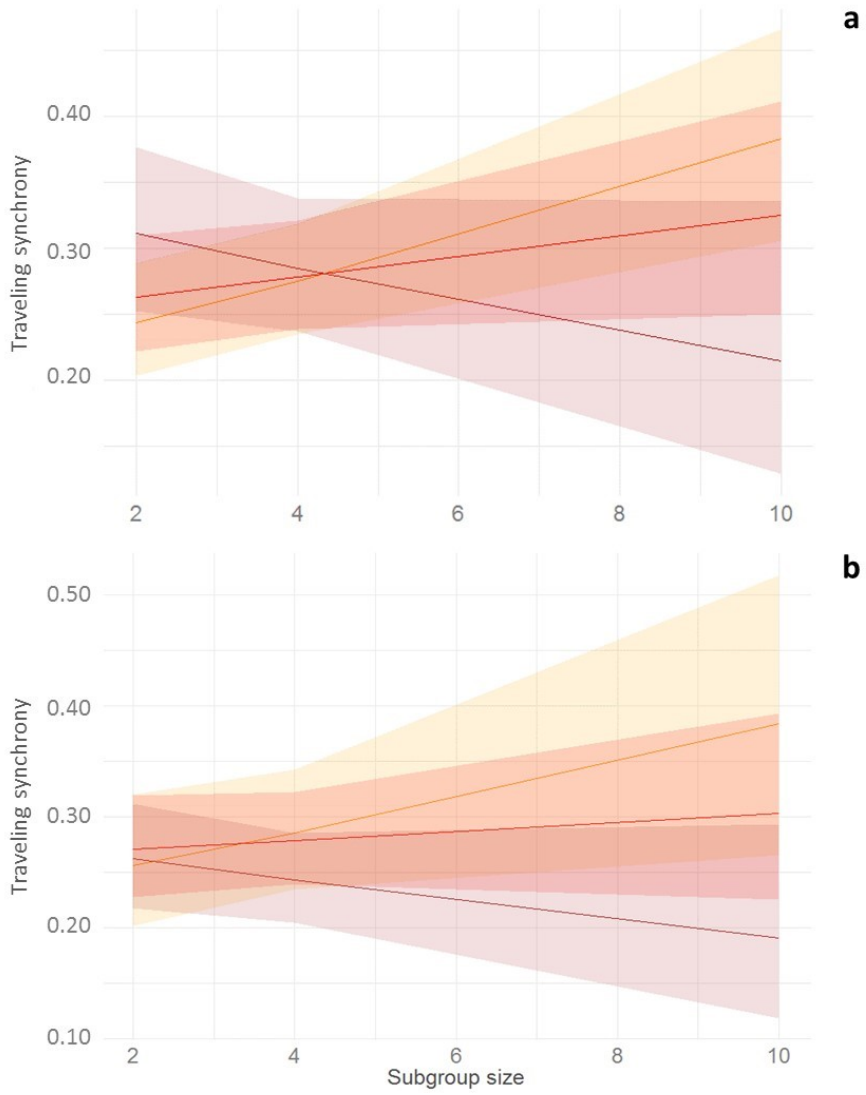


Figure 3.3. Changes of traveling synchrony with subgroup size, fruit availability and sexual composition.

Conditional plots showing that a) Traveling synchrony increased with subgroup size at low fruit availability (1st quartile of IFA values in yellow) and decreased at high fruit availability (3rd quartile of IFA values in brown), b) Traveling synchrony increased with subgroup size in subgroups composed by only males and decreased in subgroups composed only by females. Female proportion in yellow = 0, Female proportion in brown = 1.

3.5.2 Behavioral synchrony and spatial cohesion

Inter-individual distances in dyads ranged from 0 to 115 m, with a median of 15 m. The female-female dyads were the most frequent (54.12%), followed by female-male dyads (31.35%) and the male-male dyads (14.52%). However, male-male dyads had the shortest inter-individual distances (14 ± 13 m), followed by the female-female dyads (18 ± 15 m), and the female-male dyads (21 ± 16 m; Wilcoxon signed rank test, T = 1315, df = 2, $P < 0.001$).

Dyadic synchrony varied with fruit availability and inter-individual distances. Mixed and homogeneous dyads decreased when fruit availability increased, but it decrease less pronounced in male-male dyads. As expected, dyadic synchrony decreased as inter-individual distances increased in all the sex-class dyads. However, the decrease in synchrony was more pronounced in the male-male dyads (Fig 3.4).

Table 3.9. Parameters of the best model explaining dyadic synchrony of spider monkeys in OMYK.

Explanatory variable	Estimate	SE	*Z*	*P*
(Intercept)	**1.442**	**0.030**	**47.917**	**0.000**
IFA	**-0.199**	**0.016**	**-12.288**	**0.000**
Female-male	**-0.196**	**0.047**	**-4.149**	**0.000**
Male-male	**0.333**	**0.069**	**4.799**	**0.000**
IID	**-0.017**	**0.000**	**-17.147**	**0.000**
IFA x Female-male	-0.006	0.025	-0.255	0.799
IFA x Male-male	**0.09**	**0.037**	**2.415**	**0.016**
IID x Female-male	0.000	0.001	-0.193	0.847
IID x Male-male	**-0.011**	**0.002**	**-4.579**	**0.000**

* Best model: Dyadic synchrony ~ IFA + sexual composition + IID + IFA × sexual composition + IID × sexual composition. Bold characters indicate variables with a significant effect.

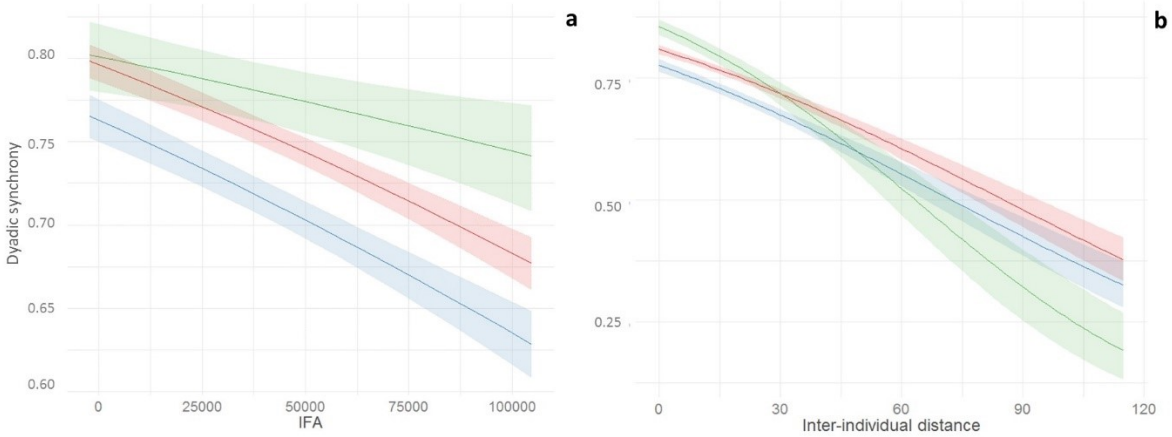


Figure 3.4. Changes in dyadic synchrony with fruit availability and inter-individual distances according to its sexual composition.

a) Conditional plot showing that dyadic synchrony decreased with the increase of fruit availability in the three types of dyads but more slightly in male dyads (female-female in red, female-male in blue, and male-male in green), b) dyadic synchrony decreased with the increase of the inter-individual distances in the three types of dyad, especially in the male-male dyads. IFA = Index of Fruit Availability.

3.6 Discussion

3.6.1 Behavioral synchrony related to environmental, social, and internal factors

We tested the influence of fruit availability, subgroup size, sexual composition, and time of the day on behavioral synchrony in spider monkeys. Behavioral synchrony was tested including all the activities (synchrony for all activities), and also by activity (feeding, traveling and resting). We found that all these factors influenced behavioral synchrony but in different intensities and importance. For instance, food availability and subgroup size were the factors that influenced most behavioral synchrony in spider monkeys. We also found that feeding, traveling and resting synchrony responded differently between the two studied groups, particularly to fruit availability and subgroup size.

In synchrony for all activities, both groups tended to present a higher synchrony when fruit availability increased. This suggests, as expected, that higher fruit availability helps to reduce foraging competition and conflict of interests among group members, and then permits consensus in activity coordination (Smith *et al*., 2008, Sueur *et al*., 2011). Pinacho-Guendulain and Ramos-Fernández (2017) found that at high fruit availability of *Brosimum alicastrum*, the most important food species at OMYK, subgroups of spider monkeys tended to be more stable and cohesive, conditions that could lead to a higher behavioral synchrony. We also found that synchrony for all activities decreased as expected when subgroup size increased. However, group B presented more difficulty in remaining synchronized than group A. This result could be due to group size in B (16) being larger than in A (10) possibly leading to conflicts of interest and to a lack of consensus (Chapman et al. 1995). Moreover, higher fruit availability should facilitate synchrony (Smith *et al*., 2008; Sueur *et al*., 2011). Other studies have

found higher behavioral synchrony in smaller subgroups compared to larger ones (i.e. Yukushima macaques, *Macaca fuscata yakui*; Agetsuma, 1995; goats, *Capra hircus*; Calhim *et al*., 2006; bachelor herds of muskoxen, Côté *et al*., 1997). This can be due to a higher probability to find individuals doing different activities in larger groups and subgroups, and also because in larger subgroups, inter-individual distances increase, leading to lower visual information and information exchange (Dostálková and Špinka, 2007; Conradt and List, 2009; Sugiura *et al*., 2010).

Contrary to our predictions, the proportion of females in subgroups did not affect synchrony for all activities in a significant way, similar to results for muskoxen (Côté *et al*., 1997). However, in sheep (Michelena *et al*., 2006) the highest synchrony has been observed in male-only groups. A simple metric like female proportion could be hiding important information such as differences among females with regard to their reproductive states, yielding an overall neutral effect of female proportion on behavioral synchrony. Distinguishing between pregnant, lactating and fertile females might reveal different patterns since females in a same reproductive state share similar requirements and are more likely to synchronize their activities (King and Cowlishaw, 2009).

Synchrony for all activities remained stable throughout the day in group A and increased slightly at the end of the day in group B. On the contrary, King and Cowlishaw (2009) found a higher behavioral synchrony for baboons (*Papio ursinus*) in the morning and a decrease throughout the day. These authors suggested that early in the day baboons are hungry, promoting synchrony in foraging and travel. This is consistent with the higher feeding synchrony we found in the morning, but not with the constant traveling synchrony. Maybe our results for synchrony for all activities are influenced by the strong increase of resting synchrony at the end of the day. Synchrony for all activities hides important particularities of each behavior that respond distinctly to the environmental, social and internal factors as showed in our results.

Environmental conditions can exert changes in feeding synchrony. For instance, fruit availability was higher in the area of activity of group B, compared to group A. We believe this difference may explain why feeding synchrony was overall higher in group A than in group B and why it increased with increasing fruit availability in group A, while it decreased in group B. Probably the lower fruit availability in group A caused a higher aggregation of individuals in fruiting trees, leading to a higher synchrony for this activity. Harrison (1985) found in green monkeys (*Cercopithecus sabaeus*) that with higher food availability animals are not necessarily more synchronized, but rather it is the ephemeral fruit production of certain species what triggers synchrony. This suggests that group A could be responding more actively to the changes in fruit availability and feeding on them when available.

Feeding synchrony decreased with subgroup size in both groups. This result is consistent with studies measuring grazing time (Agetsuma, 1995; Michelena *et al*., 2006), and suggests that it could be a way to minimize scramble competition (Wrangham *et al*., 1993; Chapman and Chapman, 2000). The proportion of females in a subgroup was the third most important factor influencing feeding behavior, which varied as expected for both groups but more markedly for group A, where feeding was more synchronized in homogeneous subgroups. This result is similar to findings of studies with ungulates (Conradt, 1998; Conradt and Roper, 2000) and baboons (King and Cowlishaw, 2009). It likely relates to the different nutritional requirements and digestive abilities of each sex (foraging selection hypothesis, Bourgoin *et al*., 2018), and to preferences for the same sex (social preference hypothesis, Ruckstuhl and Neuhaus, 2000; Bourgoin *et al*., 2018).

Feeding synchrony oscillated during the day, but was higher, as expected, in the morning, and then in late afternoon. Baldellou and Adan (1997) found a similar pattern for vervet monkeys (*Cercophithecus aethiops*) whose diet (e.g. acacia seed, foliage, gum; Butynski, 2002) differs from that of spider monkeys (mainly fruits, but also leaves;

González-Zamora *et al*., 2009). According to Macleod et al. (2005), feeding at the beginning of the activity period (i.e. in the morning for diurnal animals) could be directed towards gaining body mass, while feeding at the end of the activity period could be for gaining energy reserves required for the resting period. Feeding synchrony in group B responded somewhat differently to time: this behavior was more synchronized in the morning but not in the afternoon, when they were more synchronized for resting.

Traveling synchrony was mainly influenced by fruit availability and subgroup size. Traveling synchrony increased with fruit availability in both groups, but the effect was more pronounced in group B. It is possible that high fruit availability is accompanied by a relative spatial uncertainty of food resources, leading groups to travel in synchrony to increase the probability of finding them (King, 2010; Merkle *et al*., 2015). In relation to subgroup size, spider monkeys tended to travel more synchronously when found in larger subgroups. This is consistent with the benefits of predator avoidance, food detection (Davies *et al*., 2012) and information exchange (Krause *et al*., 2002). We also found that traveling synchronization in large groups, occurred more frequently when fruit availability was lower. In contrast, when fruit availability was high, individuals in large subgroups tended to carry out different activities. This result is consistent with the proposal that traveling in large groups could facilitate the finding of food resources (Davies *et al*., 2012, Krause *et al*., 2012). It is also in accordance with a scenario of individuals reaching consensus and remaining cohesive when food patches are scarce (in Sueur's et al., 2011).

Besides the main effect of subgroup size on traveling synchrony, this predictor also interacted with female proportion: traveling synchrony increased with subgroup size in subgroups mainly composed by males, while it was low in large subgroups composed mainly by females. This could be related to the fact that in spider monkeys males spend more time traveling than females (Symington, 1988; Wallace, 2008), and that females tend to travel alone or in small groups (Aureli and Schaffner, 2008). Traveling

synchrony changed almost imperceptibly with time. Differently to us, Baldellou and Adan (1997) found that vervet monkeys (*Cercopithecus aethiops*) were more mobile in the morning and at the end of the day, when individuals are moving away or approaching the sleeping sites. However, similarly to us, Brown (2014) found that individually, spider monkeys did not change the proportion of time spent traveling between day and dusk.

Resting synchrony was higher in group B than in group A. As fruit availability was higher in B's territory, it is possible that individuals can dedicate more time for resting and therefore present a higher resting synchronization compared to group A. Resting synchrony responded mainly to subgroup size and to female proportion. In group B, as expected, resting synchrony decreased when subgroup size increased. This coincides with what Jorgensen et al., (2009) found for ewes. Also, this could confirm that the higher the number of individuals in a subgroup, more of them will have different interests and thus engage in different activities (Ruckstuhl and Neuhaus, 2000). Interestingly, resting synchrony increased with subgroup size in group A. This unexpected result could be related to the idea that in animals with low levels of aggression, an increased group size can increase tolerance among mates when resting after regrouping (Faerevik, et al., 2007). Alternatively, the contrasting response between groups could be due to other differences in the environment of the two groups, ones not studied here (e.g. presence of predators or hunters).

Contrary to our expectations, resting synchrony was higher in mixed subgroups. It is likely that resting behavior is not related with intra-group competition, such as occurs with feeding. Contrastingly, Michelena *et al*. (2006) found that sheep, under controlled experimental conditions, spent less time resting in mixed-sex than in single-sex groups. In spider monkeys, it has been found that 49% of their resting time is spent in large feeding trees (Parada-Lopez *et al*., 2017). So, probably individuals of both sexes used large trees for resting, unfortunately we did not record the size of trees where spider

monkeys were resting. Other factors related to the variation in feeding, traveling, and resting synchrony could be food patch distribution and social or kinship affiliation among individuals. We also recommend future studies considering key tree species used for feeding and resting and to assess their influence on group cohesion.

3.6.2 Behavioral synchrony and spatial cohesion

Contrary to our expectations and to our findings in MABR for group synchrony, dyadic synchrony in OMYK decreased when fruit availability increased. Pinacho-Guendulain and Ramos-Fernández (2017) in OMYK showed that when fruit availability in *B. alicastrum* was higher, subgroups tended to be more stable and cohesive. These conditions could mean higher behavioral synchrony. Probably, at the dyadic level, feeding activity requires larger inter-individual distances to avoid intragroup feeding competition, for example, in form of contests (Sugiura et al., 2011). In the case of the interaction between fruit availability and sex-composition, all the sex-class dyads presented oscillations throughout the IFA values, but female-male dyad presented more pronounced changes in synchrony. This is probably related with the differences between sexes as suggested by the hypotheses of foraging selection and the scramble competition (Ruckstuhl and Neuhaus, 2000; Bourgoin *et al*., 2018). Activity synchrony did not change with fruit availability in only-male dyads. This could be related with the higher stability, affiliative interactions, and more cooperative relationships among males than among females or among males and females, as suggested for spider monkeys (Symington, 1988; Aureli and Schaffner, 2008). This result also supports, that male subgroups are usually more synchronized than mixed-sex, and more synchronized than female subgroups (Ruckstuhl, 1998; Michelena *et al*., 2006).

Synchrony at the dyadic level, was higher at closer IID in all the sex-class dyads, which is similar to what King and Cowlishaw (2009) found with baboons about the influence

of spatial cohesiveness and behavioral synchrony. This confirms that behavioral synchrony is facilitated by shorter inter-individual distances that promote communication (Dostálková and Spinka, 2007), allelomimesis (Deneubourg and Goss, 1989) and/or social facilitation (Rifá, 1990). In relation to the influence of sex-composition, synchrony decreased more importantly with the increase of IID in only-male dyads. However, at short IID´s (0 to 30m), dyads composed by males presented higher levels of behavioral synchrony than female and mixed dyads. At those close distances, homogeneous-sex dyads present higher synchrony than the mixed-sex dyads. This is similar to results of other studies on social affinities between sexes in homogeneous vs. mixed subgroups (Conradt, 1998; Conradt and Roper, 2000; Michelena *et al*., 2006). Still, it is interesting that when IID´s are large (> 60m), males show more difficulty in remaining behaviorally synchronized, compared to the other types of dyads even though males are considered the more social sex (Aureli and Schaffner, 2008). One possible explanation is that in spider monkeys this sex ranges in larger areas, compared to females (Symington, 1988; Hartwell et al., 2014). The occupancy of larger areas implies larger inter-individual distances, and therefore a decrease in the dyadic synchrony.

We suggest that considering affiliation preferences and kinship at the individual level could also shed light on our understanding of dyadic behavioral synchrony. For example, two individuals in our focal group, named China and Lola, constituted the most recorded dyad during the study period. Those females are mother and daughter. The second most recorded dyad was composed by Marcos and Tula, who are not siblings and were of different age during the study (Marcos: subadult, Tula: adult), but still engaged in many positive social interactions. Another important dyad was composed by China and Verónica, which are members of the group before 1995 (Smith-Aguilar, 2016).

Processes like scramble competition, and social preference among sex-classes, in relation to spatial cohesion could explain variation in group coordination. While our results on two groups of spider monkeys in MABR (at the subgroup level) and one group in OMYK (at the dyadic level) are not generalizable, they still provide useful insights on the drivers of activity synchronization in a primate species with FFD, particularly considering that most available information comes from studies on highly sexually-dimorphic ungulates. Studies on the behavioral ecology of free-ranging animals under natural conditions are difficult, especially when considering many variables, but they are necessary to shed light on the factors influencing behavioral synchrony in FFD. We encourage more studies of behavioral synchrony considering social factors such as kinship and affiliation.

3.7 Acknowledgements

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CHAPTER 4

FRUIT AVAILABILITY AND SOCIAL CONSTRAINTS AS DETERMINANTS OF ASSOCIATION AND PROXIMITY PATTERNS IN THE FISSION-FUSION SOCIETY OF SPIDER MONKEYS (*Ateles geoffroyi*)

4.1 Description of the article and contribution

In the FFD of spider monkeys, spatial cohesion between individuals in a group changes continually. In this chapter, we show how individuals associate in the same subgroup and at different inter-individual distances according to fruit availability, variance of fruiting trees and the sex of the individuals. We use social network metrics that allow revealing the interplay between environmental and social factors influencing association and proximity patterns. Only a few previous studies have tested the relationship between social network metrics and more than one independent variable. Our study also assessed these relationships at two social scales (subgroups and dyads). For instance, at the subgroup level, environmental factors were more strongly related to association patterns than were social factors, and environmental and social factors influenced the association patterns; while social factors were more important than environmental factors at the dyadic level for proximity patterns.

In this chapter I contributed with the initial idea that was further improved through discussions with Braulio Pinacho-Guendulain and Gabriel Ramos-Fernández. Data from the long-term project at OMYK were provided by Gabriel Ramos-Fernández, Filippo Aureli, Colleen Schaffner, and Laura Vick. I built the databases on inter-individual distances with the help of Aymeric Oliveira. Sandra E. Smith-Aguilar and I calculated the social network metrics. I ran the statistical analyses, and was advised by

Gabriel Ramos, Sophie Calmé, Audrey Bourret and François Rousseu. Sophie Calmé, Gabriel Ramos-Fernández, Braulio Pinacho-Guendulain and Sandra E. Smith-Aguilar made corrections and suggestions to the manuscript. This article has been submitted to American Journal of Primatology on March 16th, 2019 considering a previous revision of the editor and reviewers of this journal. It will be re-submitted in to American Journal of Primatology in July 2019.

Fruit availability and social constraints as determinants of association and proximity patterns in the fission-fusion society of spider monkeys (*Ateles geoffroyi*)

Short running title: Association and proximity patterns in *Ateles*

Adriana R. Aguilar-Melo, Sophie Calmé, Braulio Pinacho-Guendulain, Sandra E. Smith-Aguilar, and Gabriel Ramos-Fernández

4.2 Abstract

Some social species exhibit high levels of fission-fusion dynamics (FFD) that improve foraging efficiency. In this study, shed light on the way FFD allows animal groups to cope with fluctuations in fruit availability. We propose that FFD occurs through passive processes (when aggregation patterns respond to fluctuations in fruit availability) and active processes (aggregation related to sex). To test the relationships between aggregation patterns and fruit availability, we studied a group of spider monkeys in the Yucatán Peninsula of México over three years. We identified subgroup members and estimated their inter-individual distances between through instantaneous subgroup scan sampling. We evaluated fruit availability by monitoring the phenology of the 10 most important food tree species for spider monkeys in the study site. Aggregation patterns were measured ass association and proximity metrics in subgroups using social network analyses. We showed that aggregation patterns vary between seasons, respond to changes in fruit availability and are influenced by the sex of individuals, likely reflecting biological and behavioral differences between sexes and the interplay between passive and active aggregation processes. In contrast, proximity patterns were less affected by changes in fruit availability, suggesting active processes where

social factors are more important in determining intra-subgroup spatial cohesion at the dyad level.

KEYWORDS: social network; sexual segregation; seasonality, fruit availability

4.3 Introduction

Individuals may be attracted to a group through mechanisms that are related to the benefits of grouping, such as minimizing travel costs while acquiring foraging advantages (Alexander, 1974; Davies, Krebs & West, 2012; Sueur et al., 2011). In some species, such as chimpanzees and spider monkeys, grouping is highly dynamic (i.e., high degree of fission-fusion dynamics, FFD), with groups splitting into subgroups that vary in size, duration, spatial cohesion, and individual membership (Aureli et al., 2008). This dynamics appears to reduce intragroup competition and social conflicts, while improving foraging efficiency in spatially and temporally variable environments (Stevenson, Quiñones & Ahumada 1998; Sueur et al., 2011).

In species exhibiting high levels of FFD, spatial cohesion patterns could be shaped by both social factors and non-social forcing factors. For instance, individuals can be attracted to resources of common interest, resulting in passive aggregation (Whitehead, 2008; Smith-Aguilar, Ramos-Fernández & Getz 2016); while aggregations could also result from the active behavior of individuals maintaining proximity with others as a consequence of social motivations like affiliation or kinship (i.e., active association; Croft et al., 2003; Social groups sensu Whitehead, 2008). Moreover, there may be an interplay between ecological and social factors, motivating the adjustment of spatial cohesion between individuals in a group (Sibbald, Oom, Hopper & Anderson,

2008). Therefore, passive and active aggregation or segregation processes may simultaneously influence spatial cohesion in a group.

Passive aggregation (or segregation) can be explained by ecological factors such as abundance and distribution of food resources (Henzi, Lusseau, Weingrill & Van Schaik, 2009; Sueur et al., 2011). Passive aggregations can occur because the same food patches attract foraging individuals (Sugiura, Shimooka & Tsuji, 2011). Yet, environments that are variables in both time (e.g. seasonality) and space (e.g. fruit distribution), individuals in a group can have experience difficulties coordinating their actions with other members, leading to passive segregation and high degree of variability in spatial cohesion (Sueur et al., 2011). For example, spatial cohesion increases with food abundance (Stevenson et al., 1998) and clumping (Chapman, Wrangham & Chapman, 1995; Sugiura et al., 2011). In contrast, spatial cohesion decreases with food scarcity and scattering (Henzi, Lusseau, Weingrill & Van Schaik, 2009; Ramos-Fernández, Boyer, Aureli & Vick, 2009; Pinter-Wollman et al., 2014; Sugiura et al., 2011).

Social factors such as affinity (preference of association with certain individuals; Couzin, 2006; Sugiura et al., 2011) or activity synchronization (activity budget hypothesis; Bourgoin, Marchand, Hewison, Ruckstuhl & Garel, 2018) can act as regulators of spatial cohesion, causing active aggregation or segregation. Watts (2005) asserts that the social attraction hypothesis (where attraction between individuals of the same class occurs to facilitate social learning; Conradt, 2005) likely best explains social and spatial segregation in chimpanzees and spider monkeys. For example, spatial cohesion increases implicitly in the context of affiliative behaviours (e.g., allogrooming; Stevenson et al., 1998; Sugiura et al., 2011; Aureli, Schaffner, Asensio & Lusseau, 2012) or relationships (e.g., female *Papio papio*, and their primary males beyond the mating context; Goffe, Zinner & Fischer, 2016; females of *A. geoffroyi* and their juveniles; Aureli & Schaffner, 2008). Active segregation can occur due to social

dissimilarities, reduced tolerance, repulsion, avoidance or desynchronization as a result of biological and behavioral differences between age or sex classes (Wrangham, Gittleman & Chapman, 1993; Conradt & Roper, 2000; Ramos-Fernández et al., 2009). Therefore, spatial cohesion can decrease in subgroups with mixed-sex composition (e.g., *Ovis aries*; Michelena, Gautrais, Gérard, Bon & Deneuburg, 2008).

Spatial cohesion within a group also varies according to the social scale (e.g., dyads at the level of proximity, subgroup, and group), with each scale providing different information about the social structure (Smith-Aguilar, Aureli, Busia, Schaffner & Ramos-Fernández, 2018) and how it varies with respect to changes in ecological or social factors. Several studies found that group cohesion at different social scales changes with environmental variables such as precipitation or food abundance (e.g. *Loxodonta africana*, Wittemyer, Douglas-Hamilton & Getz, 2005; *Papio hamadryas ursinus*, Henzi et al., 2009; *Elephas maximus*, de Silva, Ranjeewa & Kryazhimskiy, 2011; *Orcinus orca*, Foster et al., 2012; *Crocuta crocuta*, Ilany, Booms & Holekamp 2015). For instance, family groups of *Loxodonta Africana* (closely associated breeding females and their calves) were stable across seasons, whereas larger assemblages of individuals, such as kinship groups and clans, were more cohesive in rainy than in dry seasons (Wittemyer et al., 2005). In our study we considered two social scales: 1) the subgroup, which was analyzed through association patterns that are given by the occurrence of individuals in a same subgroup; and the second level is the dyad, used for analyses of proximity patterns by looking at interindividual distances within subgroups. We assume that proximity between individuals at the dyadic scale reflects the influence of social factors like relationships; while association could be influenced to a greater extent by the environmental factors affecting FFD.

The processes of active and passive aggregation (or segregation) in FFD could be due to ecological and social factors respectively, However, as ecological and social factors can act simultaneously, interplay of active and passive processes can occur during the

regulation of spatial cohesion and social organization. These active and passive aggregation processes should allow individuals within groups to cope with changes in food availability. The socioecological model has long been important for the recognition of the relationships between ecological factors and social factors such as group membership (van Schaik, 1989; Isbell & Young, 2002). Yet, the socioecological model cannot represent all social systems that have been observed in primates (see Thierry, 2008; Koenig, Scarry, Wheeler & Borries, 2013; Janson, 2015). As Isbell and Young (2002) state, primates can be remarkably flexible in their social behavior, and this flexibility can be the result of local ecological and social conditions. Janson (2015) notes the difficulty of invoking the socioecological model to explain prolonged social relationships between sexes, other than preventing infanticide. Moreover, coalitions can be formed among females, among males, or among mixed-sexed groups, but these most likely occur for different purposes (Janson, 2015). Therefore, understanding how ecological (i.e., food availability) and social factors (i.e., sex) are interrelated, together with their relative contributions to spatial cohesion in species exhibiting FFD, could inform socioecological models so they more accurately represent the important sources of variation in social systems.

In this study, we shed light on the proximate ecological and social mechanisms that are associated specifically with FFD in spider monkeys by analyzing association and proximity patterns at different levels of social organization (subgroups and dyads with individuals at close proximity). We also uncovered information about the selection pressures that were driving the social structure of a species exhibiting high FFD and processes of active and passive aggregation (see Ramos-Fernández et al., 2009 and Smith-Aguilar et al., 2016). For the ecological variables, we focused on food resources; for the social variables, we focused on the sex of the individuals. Our main objective was to untangle the interplay between the ecological and social variable that modify spatial cohesion in spider monkeys. We hypothesized that fruit availability and temporal variation associated with fruiting trees would exert an influence on the spatial cohesion

measured by association patterns of spider monkeys through passive aggregation processes (Ramos-Fernández et al., 2009; Pinter-Wollman et al., 2014; Smith-Aguilar et al., 2016). Furthermore, differences between sexes would influence association and proximity patterns through active processes (Conradt & Roper, 2000; Krause & Ruxton 2002; Watts, 2005). Lastly, we hypothesized that the influence of fruit availability and variation associated with fruiting trees on proximity patterns would be negligible, as a result of greater influence being exerted by active aggregation processes (Conradt & Roper, 2000; Krause & Ruxton, 2002; Hartwell, Notman, Bonenfant & Pavelka, 2014). We formulated a series of predictions for the relationship between ecological and social factors and the association and proximity patterns (Table 4.1).

Table 4.1. Predictions regarding the relationships between association and proximity patterns in spider monkeys with seasonality, fruit availability, its variability, and sex in OMYK, Yucatan, Mexico.

Independent variable	Dependent variable							
	Association					Proximity		
	AI	Density	Mod_Sex	SAF	SAM	P0	P5	CV_IID
	P>A	P	P&A			P<A		P&A
Season (Rain)	+	+	-	+	+	=	=	-
IFA_F	+	+	-	+	+	=	=	-
IFA_B	+	+	-	+	+	=	=	-
Variance_ft	-	-	+	-	-	=	=	+
ff vs fm	ff >fm	NA	NA	NA	NA	ff >fm	ff >fm	NA
mm vs fm	mm>fm	NA	NA	NA	NA	mm >fm	mm>fm	NA
ff vs mm	ff<mm	NA	NA	NA	NA	ff<mm	ff<mm	NA

* ff = female-female; fm = female-male; mm = male-male. Association and proximity variables can be more strongly related to passive compared to active processes (P>A) due to food resource distribution (Henzi et al. 2009, Ramos-Fernández et al. 2009, Pinter-Wollman et al. 2014), more strongly related to active compared to passive processes (P<A) under the social attraction hypothesis (Krause et al. 2002, Croft et al. 2003, Couzin 2006), or active and passive processes interaction (P&A). +: positive effect; -: negative effect; =: no effect. AI = Association Index, Mod_Sex = Modularity by sex, SAF = Strength of Association among Females, SAM = Strength of Association among Males, P0 = Index of association among individuals at 0m of inter-individual distance, P5 = Index of association among individuals at 5m of inter-individual distance, CVI_IID = Coefficient of Variation of the inter-individual distances among the individuals, IFA_F = Index of Fruit Availability of Ficus spp., IFA_B = Index of Fruit availability of Brosimum alicastrum; Variance_ft = Variance of fruiting trees.

4.4 Methods

4.4.1 Study species: Diet and sexual segregation

Spider monkeys are highly frugivorous (fruits comprise 77% of their diet, range 55-90%; Di Fiore, Link & Dew 2008). They feed mostly on ripe fruits, but also consume unripe fruits (Di Fiore et al., 2008; Felton, Felton, Wood & Lindenmayer, 2008; Pablo-Rodríguez, Hernández-Salazar, Aureli & Schaffner, 2015). Even when spider monkeys feed on many plants, few species constitute the bulk of their diet. In our study site, *Ficus* and *Brosimum alicastrum* alone constitute > 50% of a spider monkey's annual diet (Pinacho-Guendulain & Ramos-Fernández, 2017). *Brosimum alicastrum* represented, on average, 28.8% of the diet (yearly consumption frequency) over nine years (1997-2004), and 28.4% from August 2009 to July 2010 (min. 9.7% in 2001, max. 37.5% in 2003; Pinacho-Guendulain & Ramos-Fernández, 2017). During the same period, *Ficus* spp. represented 25.2% of the annual diet for 1997-2004 and 10.1% for August 2009-July 2010 (min. 10.1% in 2009-2010, max. 34.0% in 2000; Pinacho-Guendulain & Ramos-Fernández, 2017).

Spider monkeys (*Ateles* spp.), our study species, live in groups that are often segregated by sex (Ramos-Fernandez et al., 2009, Hartwell, et al., 2014). This pattern could be explained by differences between sexes in terms of activity budgets (Symington, 1988), association (Symington, 1990; Shimooka, 2003; Busia, Schaffner & Aureli, 2016), subgroup size (Shimooka, 2003), use of the space (Shimooka, 2005), diet (Shimooka, 2005; Hartwell et al., 2014), and sociality ("less social" females, Aureli & Schaffner, 2008). Additional differences between sexes include, for instance, regular contacts between females with young that permit social interactions among offspring (Van Roosmalen, 1980), while aggregations of males occur, given that they cooperatively defend territories from competitors to ensure exclusive access to females

and food resources (Aureli & Schaffner, 2008). In fact, males of spider monkeys direct most of their affiliative behaviors towards other males and aggressive behaviors towards females (Fedigan & Baxter, 1984).

4.4.2 Study site and study group

We studied a group of spider monkeys (*A. geoffroyi*) in the Otoch Ma´ax Yetel Kooh (OMYK) protected area, also known as Punta Laguna (20° 38′ N, 87° 38′ W, 14 m elevation), and is located on the Yucatan Peninsula, Mexico. The dominant vegetation is seasonal tropical forest in different successional stages (García-Frapolli, Ayala-Orozco, Bonilla-Moheno, Espadas-Manrique & Ramos-Fernández, 2007). This region presents two seasons: a rainy season from mid-May to mid-November (concentrating 70% of the annual precipitation), and a dry season from mid-November to mid-May. Mean annual temperature is 24.3 °C, and the mean annual precipitation is 1,120 mm (1951-2010: Sistema Meteorológico Nacional 2015).

The study group is habituated to human presence as it has been followed continuously by trained field assistants since 1997 (Ramos-Fernández, Aureli, Schaffner & Vick, 2018). All group members were individually identified through facial marks and other features. Birth and migration dates are known for all individuals except for those who were adults or juveniles in 1997 (Table 4.2). Between 2009 and 2014, we recorded 18 births and one confirmed death, immigration of four males and 12 females, emigration of three females, and nine disappearances. Because of this, the overall size of the study group varied overall from 27 to 48 individuals. For the analyses we excluded infants and juveniles because their presence in a subgroup is dependent on their mothers. Therefore, we analyzed the grouping patterns of 28 adult and sub-adult monkeys (20 females and eight males, see Table 4.2). Sub-adults are individuals between 60 - 108 months of age who can forage in the same subgroup or in a subgroup

from that of their mother (Vick 2008). Typically, sub-adult females emigrate from their natal group and sub-adult males remain associated strongly with other adult and sub-adult males (Shimooka et al. 2008). Individuals are considered adults after 108 months of age, but this definition was modified to include females after their first conception, and in the case of males, when their testes have fully descended (Vick 2008).

Table 4.2. Individual characteristics of spider monkeys at OMYK during the study.

ID	Sex	Age			Migrations and deaths
		2009-2010	2013	2014	
AM	Female	Adult	Adult	Adult	
CH	Female	Adult	Adult	Adult	
FL	Female	Adult	Adult	Adult	
GO	Female	Adult	--	--	Disappeared 2012
JA	Female	Adult	Adult	Adult	
KL	Female	Adult	Adult	Adult	
VE	Female	Adult	Adult	Adult	
HI	Female	Subadult	Adult	Adult	
LO	Female	Subadult	Adult	Adult	
SR	Female	Subadult	--	--	Emigration 2010
LX	Female	Infant	Subadult	--	Emigration October 2013
VI	Female	Infant	Subadult	Subadult	Emigration February 2014
ME	Female	Infant	Juvenil	Subadult	
ML	Female	--	Adult	Adult	Immigration 2013
PC	Female	--	Adult	Adult	Immigration 2011
TG	Female	--	Adult	Adult	Immigration August 2011
AE	Female	--	Subadult	Adult	Immigration February 2013
BH	Female	--	Subadult	Adult	Immigration September 2012
SK	Female	--	Subadult	Adult	Immigration May 2013, Emigration April 2014
EL	Female	--	--	Subadult	Immigration 2014
AI	Male	Adult	Adult	Adult	
BE	Male	Adult	Adult	Adult	

ID	Sex	Age			Migrations and deaths
		2009-2010	2013	2014	
BO	Male	Subadult	Adult	Adult	
EG	Male	Subadult	Adult	Adult	
JN	Male	Subadult	Adult	Adult	
TL	Male	Subadult	Adult	Adult	
DI	Male	Subadult	--	--	Death 2011
MS	Male	Infant	Subadult	Subadult	

4.4.3 Behavioral and ecological data collection

Four field assistants (who worked from the debut of the long-term project in 1998), SESA, BPG, and other students, collected behavioral data following a standard methodology that had been implemented since 1998 (Ramos-Fernández, Aureli, Schaffner & Vick, 2018). Behavioral observations consisted of instantaneous subgroup scan samples taken every 20 min (Martin & Bateson, 2007) between dawn and dusk, for a total of 4 to 8 hours per day. In each scan sample we recorded subgroup size, together with the identity, sex and age class of each observed individual, and the inter-individual distances (hereafter, IID) between all subgroup members (see details below). Individuals were identified by facial marks and other unique features.

We defined a subgroup as all individuals who were observed at a distance of ≤ 30 m from at least one other subgroup member (using the chain-rule proposed by Ramos-Fernández, 2005). IID, were estimated visually and field assistants received prior training to facilitate these estimations. We evaluated the reliability of distance estimation between observers using Pearson Product-Moment correlation coefficient (r) and the Kendall's Coefficient of Concordance (*W*) (Martin & Bateson, 2007). These tests confirmed that our estimates were respectively accurate and consistent showing

no significant differences between real and estimated distances (r = 0.95, P < 0.05; W = 0.38, P < 0.00).

For this study we analyzed data from three 12-month periods: August 2009 to July 2010 (period 1), January to December 2013 (period 2), and January to December 2014 (period 3). Instantaneous scan-samples totaled 3,900 (1,300 hours) for Period 1; 2,813 (938 hours) for Period 2; and 2,992 (997 hours) for Period 3. For our analyses, we grouped the scan-sample data in two week stretches that corresponded to the phenological transect monitoring intervals, thereby totaling 68 biweekly samples (23 in Period 1; 23 in Period 2; and 22 in Period 3). Biweekly samples averaged 170 ± 58 scans (min: 47, max: 267) in Period 1, 120 ± 30 scans (min: 76, max: 201) in period 2, and 126 ± 20 scans (min: 89, max: 156) in period 3.

To relate grouping behavior to fruit availability, we assessed the variance of fruiting trees along a phenological transect of two km approximately which was monitored every second week, totaling 68 observation periods. On this transect, the same two field assistants recorded the presence/absence of fruit (ripe and unripe) in 10 trees per each of the 10 most important food species for spider monkeys at OMYK, according to their monthly diet between 1997 and 2004 (Pinacho-Guendulain & Ramos-Fernández, 2017; Table S1). In order to evaluate fruit availability, we also measured tree diameter at breast height (DBH) and stem density that was calculated for all individuals (DBH > 10 cm) of the 10 species in 48 block-transects of 100 x 2 m (200 m^2) and eight square plots of 2500 m^2 each, all of them randomly distributed and summing 2.96 ha in total (Pinacho-Guendulain & Ramos-Fernández, 2017).

4.4.4 Fruit availability and variability

We used three variables to represent fruit availability: 1) Index of Fruit Availability (IFA); 2) Index of Fruit Availability of *Ficus* spp. (IFA_F), and 3) IFA of *Brosimum alicastrum* (IFA_B). *Ficus* spp. and *B. alicastrum* are particularly important in the spider monkey´s diet (including ripe and unripe fruits, and leaves) in the study site. Additionally, the two species exhibit contrasting spatial distribution and fruiting synchrony and, therefore, adequately illustrate two extremes of the spatial and temporal variability of fruit resources: *Ficus* trees have a scattered distribution and an asynchronous phenology, whereas *B. alicastrum* trees are abundant, clumped, and exhibit synchronous phenology, with higher fruit production in the rainy season (Ramos-Fernández & Ayala-Orozco, 2003; Fig. 4.1).

We calculated the IFA of the 10 most important food species, following Smith-Aguilar et al. (2016), as:

Formule 4.1. $$IFA_i = \Sigma_{i=1} DBH_i \times D_i \times (TF_i / T_i)$$

Where $\sum DBH_i$ is the summed DBHs of the trees of species *i*, D_i is the density per hectare of species *i* (expressed in number of trees per ha), TF_i/T_i represents the proportion of trees of species *i* that are fruiting (TF_i) in the sample T_i. For fruiting we considered ripe and unripe fruits, given that both types are consumed by spider monkeys (Felton et al. 2008; Pablo-Rodríguez et al. 2015). We also calculated this index for *B. alicastrum* (IFA_B) and for *Ficus* spp. (IFA_F) separately. IFA and IFA_B were strongly correlated ($r = 0.94$, $p < 0.001$), prompting us to exclude IFA from further analyses to avoid collinearity. Table 4.3 provides the description and justification of the independent variables that are related to fruit availability.

Heterogeneity in fruit availability among- and within-species at a given time was represented by the Variance in the number of fruiting trees in the 10 species that were monitored (hereafter, referred to as Variance_ft). Variance_ft was calculated from the 100 trees (10 trees each of the 10 most important food species) that were monitored every second week along the phenological transects.

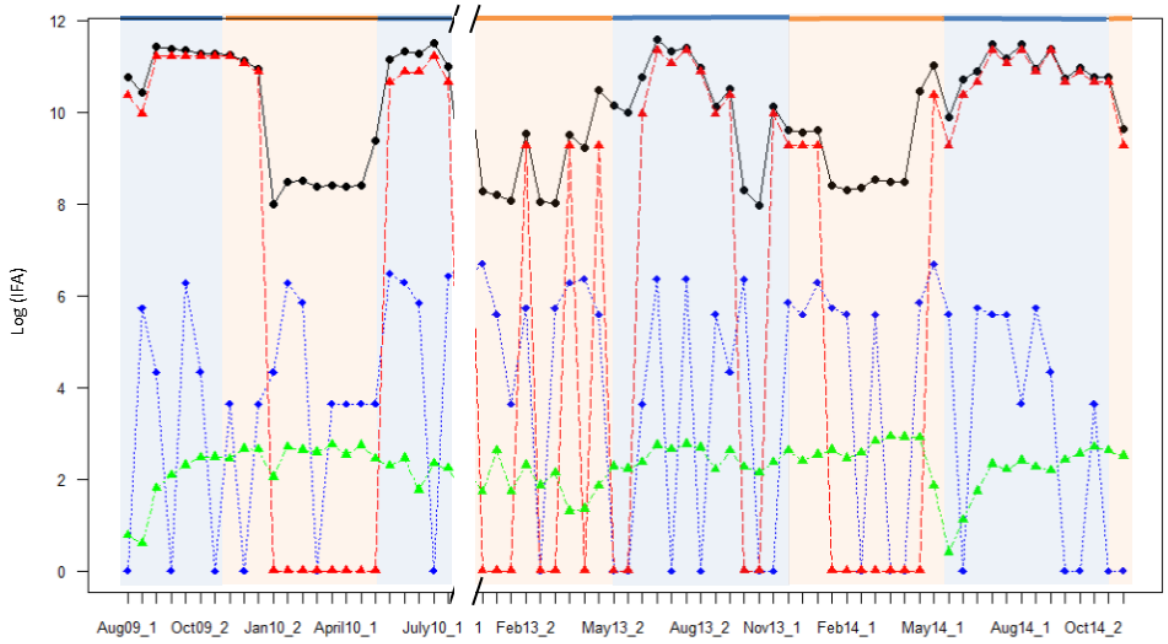

Figure 4.1. Indices of fruit availability and variance of fruiting trees, and their variation during the study periods and seasons.

Note that the Y-axis is logarithmic. Black line and circles represent the Index of Fruit Availabilty and the top ten food species in OMYK (IFA); red line and triangles represent the Index of Fruit Availability of *Brosimum alicastrum* (IFA_B); blue line and diamonds show the Index of Fruit Availability of *Ficus* spp. (IFA_F); green line and triangles represent the Variance of fruiting trees. Rainy seasons are shaded blue and dry seasons

are shaded orange. Note that high levels of fruit availability in *B. alicastrum* coincide with the rain seasons.

Table 4.3. Definition and justification of explanatory variables used to quantify the influence of food availability on the association and proximity patterns in spider monkeys at OMYK.

Explanatory variable	Definition (units)	Justification
Season	Rainy or Dry season	The pattern is seasonal, with 70% of annual precipitation occurring during the rainy season, which lasts 6 months (Sistema Meteorológico Nacional, 2015).
IFA	Fruit availability of the 10 most important food species for spider monkeys in the study site	Important food resources for spider monkeys (Pinacho-Guendulain & Ramos-Fernandez, 2017).
IFA_F	Fruit availability of *Ficus* spp. trees measured every second week (see Methods)	Important food resource for spider monkeys with a scattered spatial distribution in OMYK that represents 25% of the spider monkeys diet between 1997 and 2004 (Pinacho-Guendulain & Ramos-Fernandez 2017).
IFA_B	Fruit availability of *Brosimum alicastrum* trees measured every second week (see Methods)	Important food resource for spider monkeys with a clumped spatial distribution in OMYK that represents 29% of the spider monkeys diet between 1997 and 2004 (Pinacho-Guendulain & Ramos-Fernandez 2017).
Variance_ft	Variance of fruiting trees of the 10 most important food species for spider monkey in the study site	Represents heterogeneity in the foraging environment, through variability in fruit availability.

4.4.5 Dyad composition

With the information on the identity and sex of the individuals, we created a social variable to describe the sex composition of dyads. We define dyad as the association of two individuals simultaneously present in a same subgroup in the same instantaneous scan sample. Three types of dyads are possible: 1) female-female (f-f); 2) male-male (m-m); and 3) female-male (f-m). We denoted this variable Sex_dyad.

4.4.6 Association and proximity patterns

We defined the association between two individuals as their simultaneous presence in the same subgroup in a given instantaneous sample (Table C2). Proximity patterns were based on two categories of inter-individual distances between pairs of monkeys in a same subgroup: 0 m (individuals in contact) and 5 m (± 2 m) (Table C2). The IID class '0 m' reflects the maximum level of spatial tolerance between individuals. The IID class '5 m' also indicates tolerance, but to a lower degree as an individual still has the possibility of evading aggression within the dyad; it is an arbitrary distance that was meant to explore other potential patterns within the dyad and the subgroup derived from influences differing from IID at 0 m. Proximity has been used as a proxy for tolerance and probability of social interaction when direct observation of interactions is not possible or rare, as occurs with spider monkeys (Grabowska-Zhang, Hinde, Garroway & Sheldon, 2016). Proximity has also been used as an indicator of social relationships (Rebecchini, Schaffner & Aureli 2011; Goffe et al., 2016). Furthermore, we assumed that the absence of observed agonistic interactions between individuals potentially indicates tolerance (absence of, or low interference or contest competition; Krause et al., 2002; Davies, Krebs & West, 2012), affiliation (Krause & Ruxton, 2002; Aureli et al., 2008), and favorable ecological conditions (Dubois & Giraldeau, 2003; Sueur et al.,

2011). In contrast, relatively large distances between individuals may reflect avoidance behavior and segregation.

Association and proximity indices

We calculated three indices that were based upon the simple ratio index (Cairns & Schwager, 1987) to analyze association and proximity patterns. These indices used information from the scan samples of monkey subgroups for each 14-day sample of the study. The association index (hereafter, AI) was based upon individual co-occurrence in the same subgroup while two proximity indices were calculated using the previously described IID classes '0 m' and '5 m' (P0 and P5, respectively).

AI is the ratio of the number of scans in which two given individuals were recorded together in the same subgroup, relative to the total number of scans in which they were observed, which is expressed as:

Formule 4.2. $AI = N_{AB} / (N_{AB} + N_A + N_B)$

where N_{AB} corresponds to the number of scans during which individuals *A* and *B* were present in the same subgroup; N_A is the number of occurrences of *A* in absence of *B*; and N_B is the number of occurrences of *B* in absence of *A* (Cairns & Schwager, 1987). For these analyses, we discarded individuals who were observed in less than 10% of the scans to avoid erroneous values of AI.

We considered three variables that reflect proximity patterns based upon inter-individual distances. The first two variables (P0 and P5) were calculated in the same

manner as AI, but only with respect to the number of scans in which individuals were in contact (IID class '0 m' = 1) and at 5 ± 2 m (IID class '5 m'= 1), respectively. The third variable for proximity patterns was the coefficient of variation of all inter-individual distances (CV_IID), which was used as a measure of heterogeneity in the proximity of dyad members.

Social network metrics

We calculated network metrics for association networks that were based upon AI. We constructed undirected, weighted networks in which nodes corresponded to individuals and the edges represented the value of AI between them. A network was constructed for each two-week observation sample (totalling 68 networks), reflecting the patterns of co-occurrence between individuals for that period. Networks were constructed and analyzed using the igraph package (Csardi & Nepusz, 2006) in R version 3.5.2. (R Core Team, 2015).

We used four network metrics to analyze association patterns: 1) Density, which represents the tendency of individuals to form social ties and is calculated as the ratio of the number of observed edges (when two individuals were associated in the same subgroup) to the maximum number of possible edges in the network (Wasserman & Faust, 1994; Madden; Dreze; Pearce & Clutton-Brock, 2009; Table C2); 2) Modularity by sex (Mod_Sex), which measures individual segregation by sex class, by quantifying the presence of same-sex modules within the network (Brandes et al., 2008; Kasper & Voelkl, 2009; Table S2); 3) Strength of association among females (SAF) (Vertex strength centrality, Kasper & Voelkl, 2009; Table S2); and 4) Strength of association among males (SAM) (Vertex strength centrality, Kasper & Voelkl, 2009; Table S2). 'Strength' is the sum of all the edge weights of each node (Kasper & Voelkl, 2009). Density (as the tendency to form social ties) and Mod_Sex (as an indicator of sexual

segregation) are global measures for each network and are related to their structure, while SAF and SAM are calculated for each individual in the network. Strength of association among females and among males was estimated in R, using the formula proposed by Kasper & Voelkl (2009).

4.4.7 Statistical analyses

We used generalized mixed models to test the relationship between the indices of association (AI) and proximity (P0, P5, CV_IID) or the network metrics (Density, Mod_sex, SAM and SAF) and fruit availability and its variability (IFA_F and IFA_B, Variance_ft). We also included the variable Sex_dyad as an explanatory variable in the analyses for AI, P0 and P5, because the sex of the individuals is not accounted or in these indices as it is in the network metrics using the dyad level (i.e. Mod_sex, SAM and SAF). The other explanatory variables are related to fruit resource availability and its variability in space (patterns of aggregation of *Ficus* spp. and *B. alicastrum*) and time (periods of fruiting). We also included season as an independent variable because climate in our study site is highly seasonal.

Given that AI, P0, and P5 often contained values equal to 0 (no association between individuals), they showed non-normal errors near bounds 0 or 1. We used a beta regression distribution when running these models, performing a transformation to limit the data to the 0-1 interval (Smithson & Verkuilen, 2006).

We constructed a series of models for each response variable, considering the following interactions between explanatory variables: Season×IFA_B, Season×IFA_F, Season×Variance_ft, IFA_B×IFA_F, IFA_B×Variance_ft, IFA_F×Variance_ft, and Sex_dyad×IFA_B, Sex_dyad×IFA_F, Sex_dyad×Variance_ft in the case of AI, P0 and

P5. Random effects were Season by year and dyad or individual, depending on the response variable in the models. Interactions between explanatory variables were included considering that the variance of fruiting trees may occur simultaneously with fruit availability in *B. alicastrum* and in *Ficus* spp. We fitted the models using the glmmTMB package (Brooks et al., 2017) for AI, P0 and P5, and the lme4 package for the remaining indices (Bates, Machler, Bolker & Walker, 2014). We performed all analyses in R version 3.5.2 (R Core Team, 2018). To select the best models, for AI, P0 and P5, we began with the most saturated model and then used backward elimination to sequentially remove the variable with the highest *P*-value using the criterion *α* (Bolker, 2007). For Density, Mod_sex, SAF, SAM and CV_IID, we used backward elimination using confidence intervals (2.5% - 97-5%). We compared each new model to the previous one with a likelihood-ratio test (Bolker, 2007).

4.4.8 Ethical standards

We conducted the present study in accordance with the guidelines of the Department of Environment and Natural Resources of Mexico (SEMARNAT) under Research Permits DGVS1752/09, DGVS009/13 and DGVS02716/14, and the guidelines of the Canadian Council on Animal Care in Science under permit SC-2014-01 of the Animal Experimentation Ethics Committee of the Université de Sherbrooke. None of the authors had physical contact with the primates in the study area. This study adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

4.5 Results

4.5.1 Association patterns

Individuals were more strongly associated in a same subgroup in 2009-2010 (mean AI = 0.137 ± SD 0.18), than in 2013 (0.105 ± SD 0.171) and 2014 (0.112 ± SD 0.160) (F = 97.33, df = 2, N =11886, P < 0.001). Networks were denser (individuals tended to form more ties by network) in 2014 (0.890 ± SD 0.030) than in 2009-2010 (0.880 ± SD 0.028) and 2013 (0.868 ± SD 0.029) (Kruskal-Wallis H = 17.1, df = 2, n = 68, P < 0.0001).

As expected, the association among individuals (AI) tended to respond not only to changes in fruit availability, but also to the composition of the dyads. Individuals were more associated in rain season when fruit availability was higher in the species with a clumpy distribution and seasonal phenology (*B. alicastrum*; Table 4.4, Fig. 4.2 A). In the rainy season, spider monkeys associated more strongly when the variance of fruiting was low (i.e., a few trees of most species were fruiting), but in dry seasons the reverse was true (Table 4.4, Fig. 4.2 B). Furthermore, association among individuals increased with *Ficus* spp. fruit availability, but only when fruit availability was high for *B. alicastrum*; it decreased for lower *B. alicastrum* fruit availability (Table 4.4, Fig. 4.2 C). Association among individuals increased with *Ficus* fruit availability, but only at low variance of fruiting trees (Table 4.4, Fig. 4.2 D). For all types of dyads, association among individuals decreased with increasing variance of fruiting trees; this tendency was more pronounced in male dyads (Table 4.4; Fig. C1). All types of dyads also associated slightly more strongly in the dry season than in the rainy season (Table 4.4).

Network density (Density), which is a measure of association between all the possible dyads in the group, decreased at higher variance of fruiting trees, especially in the rainy season (Table 4.5, Fig. C2B). Full models and *P*-values of the variables for AI and Density are summarized in Tables C3 and C4.

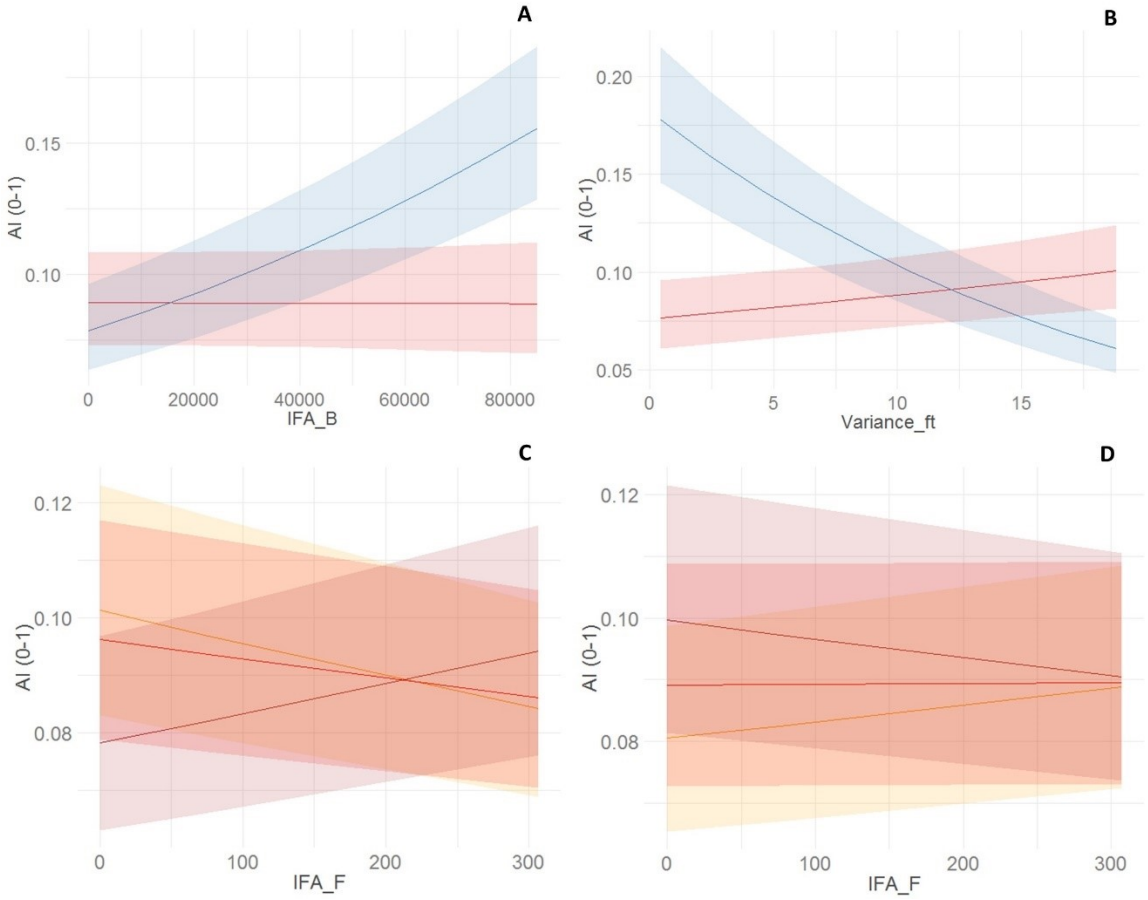

Figure 4.2. Changes of association among spider monkeys with the environmental factors.

A: Contrast plot showing that association among spider monkeys increased in rainy seasons (blue line) when fruit availability in *B. alicastrum* (IFA_B) increased; no effect was found in dry seasons (red line). B: Contrast plot showing that association among spider monkeys

decreased in rainy season (blue line) when variability of fruit availability between trees and between species (Variance_ft) increased. Association among spider monkeys increased slightly in dry seasons when variance of fruiting trees (Variance_ft) increased. Bands in colors represent the confidence bands. C: Conditional plot showing that association among spider monkeys increased with fruit availability in *Ficus* spp. (IFA_F) at high values of *B. alicastrum* (IFA_B). However, the association among spider monkeys decreased when IFA_B was lower even when IFA_F increased. D: Association among spider monkeys increased with fruit availability in *Ficus* spp. at low variability of fruit availability between trees and species (Variance_ft), but decreased at high Variance_ft. In C and D: Orange line indicates values near the first quartile of IFA_B in C and of Variance_ft in D, red line indicates values near the median of IFA_B and Variance_ft respectively, and brown line indicates the third quartile. Bands in colors represent the confidence bands.

Table 4.4. Parameters of models explaining associations (AI) in spider monkeys at OMYK.

Independent variable	Estimate	SE	Z	*P*-value
(Intercept)	-2.325	0.112	-20.682	0.000
Rain	0.122	0.042	2.928	0.003
IFA_F	0.012	0.011	1.080	0.280
IFA_B	-0.001	0.028	-0.054	0.957
Variance_ft	0.067	0.022	3.073	0.002
Female-male	-0.301	0.100	-3.057	0.002
Male-male	0.187	0.177	1.060	0.289
Rain x FA_B	**0.275**	**0.034**	**8.007**	**0.000**
Rain x Variance_ft	**-0.335**	**0.030**	**-11.316**	**0.000**
IFA_F x IFA_B	**0.173**	**0.011**	**15.860**	**0.000**
IFA_F x Variance_ft	**-0.125**	**0.012**	**-10.579**	**0.000**
Variance_ft x Female-male	-0.033	0.021	-1.551	0.121
Variance_ft x Male-male	**-0.082**	**0.033**	**-2.458**	**0.014**
Rain x Female-male	**-0.209**	**0.042**	**-5.005**	**0.000**

* The best model for AI was: AI ~ Season + IFA_F + IFA_B + Variance_ft Sex_Dyad + Season×IFA_F + Season×IFA_B + Season×Variance_ft + Sex_Dyad×IFA_F + Sex_Dyad×IFA_B + Sex_Dyad×Variance_ft IFA_F×IFA_B + IFA_F×Variance_ft + (1|Dyad) + (1|Season by year). IFA_F = Fruit availability in Ficus spp., IFA_B = Fruit availability in B. alicastrum, Variance_ft = Variance of fruiting trees. Boldface type indicates statistical significance P values.

Table 4.5. Parameters of the model explaining Network Density (Density) in spider monkeys at OMYK.

Independent variable	Estimate	SE	*t*	95% CI		
(Intercept)	0.886	0.010	90.632	0.869	-	0.903
Season (Rain)	-0.014	0.015	-0.960	-0.039	-	0.011
IFA_F	-0.005	0.004	-1.329	-0.011	-	0.003
IFA_B	0.007	0.005	1.374	-0.003	-	0.014
Variance_ft	-0.005	0.006	-0.791	-0.008	-	0.011
Rain×Variance_ft	**-0.013**	**0.009**	**-1.485**	**-0.032**	**-**	**-0.003**

* The best model for Density was: Density ~ Season + IFA_F + IFA_B + Variance_ft + Season×IFA_F + Season×IFA_B + (1|Season by year). Bold type indicates variables with a significant effect. IFA_F = Fruit availability in Ficus spp., IFA_B = Fruit availability in B. alicastrum, Variance_ft = Variance of fruiting trees.

4.5.2 Association patterns with sex as a constraint

Our results suggested that fruit availability influences sex segregation and association among same-sex individuals, and that each sex responds differently. Modularity by sex, a measure of sexual segregation in the association network, was affected by ecological variables, but in some cases not as would be expected. For instance, contrary to our predictions, spider monkeys tended to be more segregated by sex at higher fruit availability in *Ficus* spp. or when fruit production was more variable among species and individual trees in the rainy season (i.e., when Variance_ft was high), while the reverse was true in the dry season (Table 4.6, Fig. 4.3).

Interaction effects between fruit availability in *B. alicastrum* and in *Ficus* spp., or between fruit availability in *B. alicastrum* and the variance of fruiting trees, were weak with respect to sexual segregation, but significant (Table 4.6; Fig S3A and S3B). High *B. alicastrum* fruit availability had a stronger effect on sexual segregation, with spider monkeys less segregated by sex (low Mod_sex) when *Ficus* spp. fruit availability was high (Fig. S3A). The same pattern occurred for the interaction between *B. alicastrum* fruit availability and variance of fruiting trees, with individuals of different sexes being less segregated under conditions of high *B. alicastrum* fruit availability and high variance of fruiting trees (Fig. C3B).

The strength of association among females (SAF) and among males (SAM) responded to changes of fruit availability (Table 4.7; Fig. 4.4). As expected, association among females decreased with variance in fruiting trees (Variance_ft), but this was true only during the rainy season; during the dry season, the opposite occurred (Table 4.7, Fig. 4.4 A). Similarly, association among males increased with fruit availability in *B. alicastrum*, but only during the dry season (Table 4.7, Fig. 4.4 B). Other significant changes in association among females and among males occurred, but these were weak (Fig. C4). For instance, association among males changed in opposite directions with variance of fruiting trees: it increased at low-medium availability of *B. alicastrum*,

but decreased at high availability (Table 4.7, Fig. C4A). Full models and their *P*-values for Modularity by sex, Strength of Association among females and among males are summarized in Tables C5, C6, and SC7.

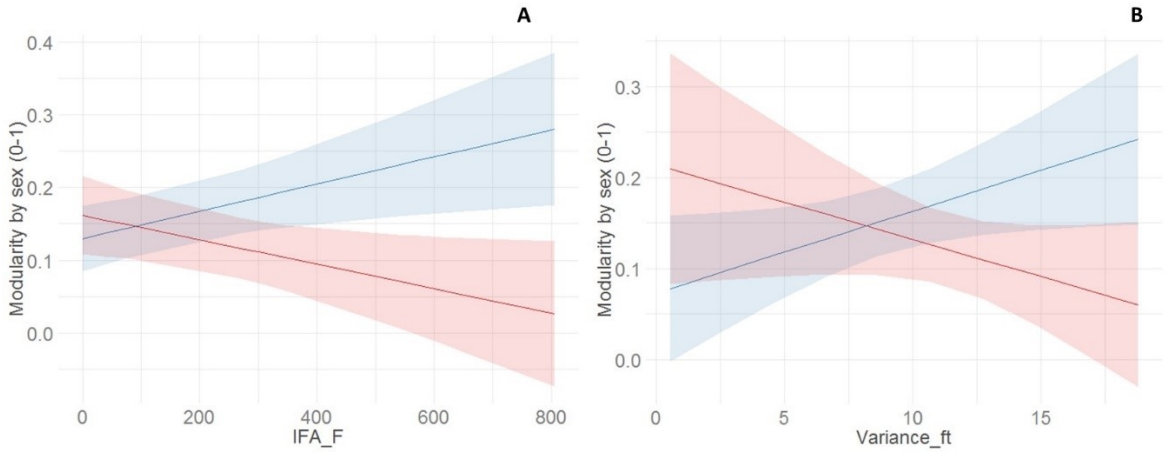

Figure 4.3. Changes in sexual segregation with seasons, *Ficus* fruit availability and Variance of fruiting trees.

A: Contrast plot showing that sexual segregation in spider monkeys increased with *Ficus* fruit availability (IFA_F) in rainy seasons (blue line), while it decreased in dry seasons (red line). B: Contrast plot showing that sexual segregation increased with variability of fruit availability between trees and between species (Variance_ft) in rainy seasons (blue line), but it decreased in dry seasons (red line). Colored bands represent the confidence bands.

Table 4.6. Parameters of the models explaining segregation by sex (Network Modularity by Sex, Mod_Sex) at OMYK.

Independent variable	Estimate	SE	*t*	95% CI		
(Intercept)	0.127	0.021	6.085	0.093	-	0.161
Season (Rain)	0.043	0.033	1.307	-0.012	-	0.096
lFA_F	**-0.039**	**0.019**	**-2.111**	**-0.071**	**-**	**-0.003**
lFA_B	-0.010	0.015	-0.678	-0.036	-	0.017
Variance_ft	**-0.033**	**0.023**	**-1.453**	**-0.078**	**-**	**0.004**
Rain×lFA_F	**0.083**	**0.029**	**2.852**	**0.027**	**-**	**0.133**
Rain×Variance_ft	**0.069**	**0.032**	**2.185**	**0.014**	**-**	**0.131**
lFA_F×lFA_B	**-0.035**	**0.014**	**-2.494**	**-0.062**	**-**	**-0.009**
lFA_B×Variance_ft	**-0.041**	**0.018**	**-2.278**	**-0.076**	**-**	**-0.010**

* The best model was: Mod_Sex ~ Season + lFA_F + lFA_B + Variance_ft + Season×lFA_F + Season×lFA_B + Season×Variance_ft + lFA_F×lFA_B + lFA_F×lFA_B **+** lFA_B×Variance_ft **+** (1|Season by year). Bold type indicates variables with a significant effect.

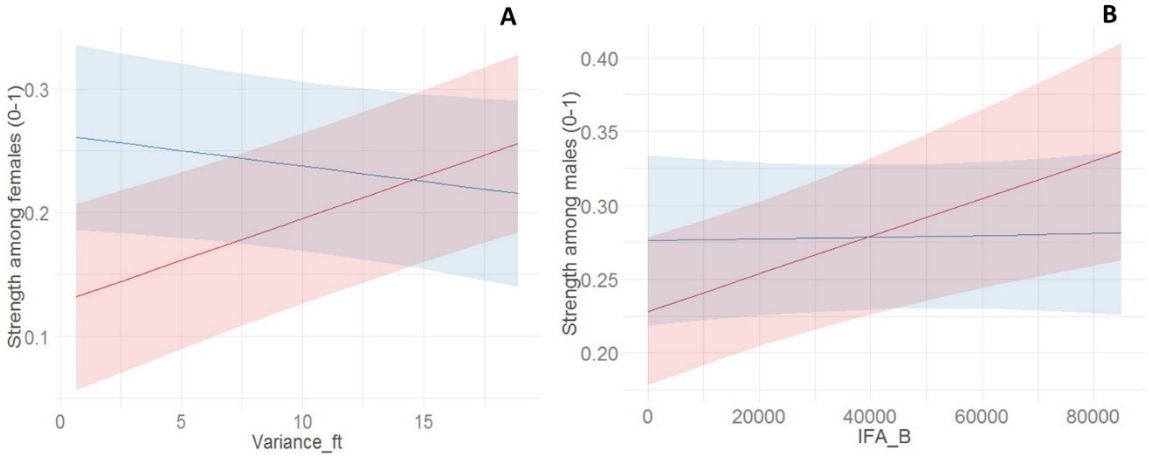

Figure 4.4. A: Changes in the strength of association among males and among males with seasons, the variance of fruiting trees and *Brosimum* fruit availability.

Contrast plot showing that strength of association among females in spider monkeys was higher in rainy seasons (blue line) at low variability of fruit availability (Variance_ft) compared to dry seasons (red line). B: Contrast plot showing that strength of association among males in spider monkeys increased with Brosimum fruit availability (IFA_B) in dry seasons (red line).

4.5.3 Proximity patterns

Association between individuals in contact (P0) was higher in 2014 (0.078 ± SD 0.201) than in 2013 (0.052 ± SD 0.133) and in 2009-2010 (0.054 ± SD 0.117; Kruskal Wallis, H = 40.83, df= 2, P<0.001). On the other hand, the association index between individuals at a distance of 5 m (P5) presented higher values in 2009-2010 (Kruskal Wallis, H = 175.43, df= 2, P < 0.001, P5 = 0.037 ± SD 0.05) than in 2013 (P5 = 0.032 ± SD 0.06) and in 2014 (P5 = 0.028 ± SD 0.06).

Association between individuals in contact (P0) and 3-7 m apart (P5) were influenced only by sex composition in the dyads (Table 4.8). Dyads of the same sex were more strongly associated than mixed dyads, and male dyads were more strongly associated than female dyads. Variability in inter-individual distances (CV_IID) decreased slightly with increasing fruit availability in *B. alicastrum* and *Ficus* spp. (Table 4.9). Full models and the *P*-values of the variables for P0, P5 and CV_IID are summarized in Tables C8 and C9 and C10.

Table 4.7. Parameters of models explaining Strength of Association of Females to Females (SAF) and Strength of Association of Males to Males (SAM), association metrics that include sex as a social constraint in spider monkeys at OMYK.

Independent variable	SAF				SAM			
	Estimate	SE	*t*	95% CI	Estimate	SE	T	95% CI
(Intercept)	0.201	0.035	7.723	0.134 - 0.268	0.267	0.030	8.795	0.209 - 0.324
Season (Rain)	0.035	0.045	0.765	-0.053 - 0.123	0.012	0.018	0.668	-0.021 - 0.045
IFA_F	**-0.022**	**0.004**	**-5.223**	**-0.030 - -0.014**	**0.027**	**0.007**	**3.936**	**0.014 - 0.041**
IFA_B	**-0.034**	**0.005**	**-6.702**	**-0.043 - -0.023**	**0.114**	**0.024**	**4.745**	**0.065 - 0.158**
Variance_ft	**0.027**	**0.006**	**4.745**	**0.016 - 0.039**	-0.000	0.002	-0.069	0.003 - 0.003
Rain×IFA_B	--	--	--	--	**-0.037**	**0.015**	**-2.479**	**-0.067 - -0.009**
Rain×Variance_ft	**-0.038**	**0.009**	**-4.312**	**-0.055 - -0.021**	**--**	**--**	**--**	**--**
IFA_F×IFA_B	**0.018**	**0.004**	**4.175**	**0.010 - 0.027**	--	--	--	--
IFA_F×Variance_ft	**-0.033**	**0.004**	**-7.798**	**-0.041 - -0.025**	**--**	**--**	**--**	**--**
IFA_B×Variance_ft	--	**--**	--	--	**-0.009**	**0.002**	**-4.511**	**-0.013 - -0.005**

* The best model for SAF was: SAF ~ Sex + Season + IFA_F + IFA_B + Variance_ft + Season×Variance_ft + IFA_F×IFA_B **+** IFA_F×Variance_ft + (1|Individual) + (1|Season by year). The best model for SAM was: SAM ~ Sex + Season + IFA_F + IFA_B + Variance_ft + Sex×IFA_F + Sex×IFA_B + Season×IFA_F + Season×IFA_B + Season×Variance_ft + IFA_F×Variance_ft **+** (1|Individual) + (1|Season by year). Bold type indicates variables with a significant effect.

Table 4.8. Parameters of models explaining the proximity metrics Simple Ratio Index at Inter-Individual Distances of 0 and 5m (±2m) (P5) of spider monkeys at OMYK.

	P0				P5			
	Estimate	SE	Z	*P*-value	Estimate	SE	Z	*P*-value
(Intercept)	0.079	0.011	7.044	0.187×10^{-12}	0.078	0.011	7.028	0.187×10^{-12}
Rain	0.010	0.011	0.926	0.3544	0.010	0.011	0.926	0.3544
IFA_F	-0.002	0.002	-0.757	0.449	-0.002	0.002	-0.757	0.449
IFA_B	-0.003	0.003	-1.247	0.212	-0.003	0.003	-1.247	0.212
Variance_ft	0.004	0.003	1.395	0.163	0.004	0.003	1.395	0.163
Female-male	**-0.061**	**0.012**	**-5.299**	**0.116×10^{-07}**	**-0.061**	**0.012**	**-5.299**	**0.116×10^{-07}**
Male-male	**0.045**	**0.019**	**2.362**	**0.018**	**0.045**	**0.019**	**2.362**	**0.018**

* The best model for P0 and P5 was: ~ Season + IFA_F + IFA_B + Variance_ft + SexDyad (1|Dyad) + (1|Season by year).

Table 4.9. Parameters of models explaining the proximity metric Coefficient of Variation of Inter-Individual Distances (CV_IID) of spider monkeys at OMYK.

Independent variable	CV_IID					
	Estimate	SE	*t*	95% CI		
(Intercept)	0.804	5.935	13.551	69.484	-	9.124
Season (Rain)	4.014	7.506	0.535	-9.958	-	1.799
IFA_F	**-0.009**	**4.443**	**-2.125**	**-0.018**	**-**	**-0.000**
IFA_B	**-0.009**	**0.000**	**-2.178**	**-0.000**	**-**	**-0.000**
Variance_ft	0.123	0.305	0.404	-0.500	-	0.689

* The best model for CV_IID was: CV_IID ~ Season + IFA_F + IFA_B + Variance_ft + (1|Season by year). Bold type indicates variables with a significant effect.

4.6 Discussion

Our results indicated that both passive and active processes of aggregation affected association and proximity patterns of spider monkeys, and ultimately their fission-fusion dynamics. We have shown that association patterns, which reflect spatial cohesion at the subgroup level, respond not only to changes in fruit availability, but are also influenced by differences between individuals, especially with respect to their sex. In contrast, proximity patterns, which reflect spatial cohesion at the dyad level, were affected by the sex of the individuals but were minimally affected by changes in fruit availability. Throughout our results, we confirmed that the males in spider monkeys associate more actively than do the females, and that the females tended to associate less selectively (Symington, 1990; Ramos-Fernández et al., 2009, but see differences among seasons in Shimooka, 2003).

4.6.1 Association patterns

The association between individuals in the same subgroup was affected by seasonality and fluctuations in fruit availability. This is what would be expected if individuals aggregated and segregated through passive processes. For instance, during the rainy season, spider monkeys aggregated *B. alicastrum* a species that fruits synchronously during that season (Figure 4.1), and which exhibits a clumped distribution. The influence of passive processes of aggregation is consistent with the lower fission-fusion rates when *B. alicastrum* was fruiting, as previously observed by Pinacho-Guendulain & Ramos-Fernández (2017) in the same study site. However, in the rare periods when *B. alicastrum* was not fruiting in the rainy season, monkeys likely faced higher uncertainty regarding other food trees with scattered distributions (e.g., *Metopium brownei* and *Spondias mombin*). Consequently, individuals would have difficulties in

reaching consensus regarding movement decisions (as suggested by Sueur et al., 2011), thereby leading to passive segregation.

Segregation (lower association index) among individuals occurred at high variability of fruit availability among trees and among species, when fruit availability of *Ficus* (the scattered species with asynchronous phenology) increased. Spider monkeys also tended to segregate (lower Density) passively during the rainy season, when fruit productivity was highly variable among trees and species (high Variance_ft). In this season, fruits of *B. alicastrum* are scarce, leading individuals to aggregate in the trees of the few fruiting species (e.g., *Manilkara zapota*). Food scarcity also likely led to greater association rates in Asian elephant (*Elephas maximus*) during the dry season, probably as a result of individuals co-occurring in resource sites (da Silva, Ranjeewa & Kryazhimskiy, 2011). This response is also similar to what Ilany et al. (2015) found in clans of hyenas (*Crocuta crocuta*), where network density was lower when prey had scattered distributions (though this happened during drier years). This could mean that a high variability in fruit availability promotes passive dispersion and, therefore, less contact between individuals within a group. This situation likely corresponds to the scenario that was proposed by Sueur et al. (2011) in which uncertainty about the location of available food sources occurs and individuals struggling to reach a consensus tend to disperse for foraging.

4.6.2 Modularity by sex, Strength among females and Strength among males

Segregation among sexes changed with seasons and fruit availability. This suggests that sex intervenes as a social constraint for grouping and indicates the interplay between passive and active processes of aggregation in spider monkeys. Individuals of both sexes tended to be more segregated at high fruit availability in *Brosimum alicastrum* (species with a clumped distribution and asynchronous phenology; Fig.

4.3A) and high variability in fruit availability among trees and species (Fig. 4.3B), but this was true only during the rainy season. Sexual segregation due to uncertainty of fruit availability could enhance the differences in diet, activity budgets, use of space, association between sexes, and social preferences of spider monkeys (Symington, 1990; Aureli & Schaffner, 2008; Hartwell et al., 2014, 2018). A possible explanation in our case is that when *Brosimum alicastrum* fruit availability increased in the rainy season, females likely remained in these important feeding trees (Pinacho-Guendulain & Ramos-Fernández, 2017), while males might find other fruiting species when patrolling the territory.

Our results on association strength among females and among males also reflected differences between sexes that depend upon the environment and which facilitate sex segregation. We confirmed that associations among males are more stable, whereas associations among females vary more strongly with ecological variables. For instance, the association among females decreased in the rainy season, but increased in the dry season with increasing variance of fruiting trees. In the rainy season, females likely associated more strongly at low variance of fruiting trees (i.e., few trees, but most species were fruiting) due to a higher abundance of food resources and more species that were in fruit (Shimooka, 2003). During the dry season, females were more strongly segregated at low variance of fruiting trees, which is likely related to the lower abundance of food resources. In contrast, the stability and strength of male associations is probably related to the fact that males must patrol their territory to defend resources (Aureli & Schaffner, 2008).

4.6.3 Proximity patterns

The indices and metrics of proximity between individuals in contact or at 5 m did not vary with fruit availability or its variability. Nevertheless, individuals of the same sex

were found closer together. This suggests that individuals make active decisions to be close to specific individuals (Croft et al. 2003) and reflects the social preferences among individuals of the same sex and age (Watts 2005). In this sense, Busia et al. (2016) found that individuals prefer to interact with those whom they share high levels of compatibility (a measure of tolerance and affiliation based on a shared history of social exchanges, e.g. sex and kinship), value (benefits afforded by a relationship; e.g. food sharing and agonistic support) and security (predictability and consistency of the behavior of partners towards one another over time; e.g., mixed sex dyads).

Our statistical models also showed that individuals in male dyads were closer than in female dyads. This confirms what has been previously found for spider monkeys (Symington 1990; Ramos-Fernández et al., 2009; but see exceptions in some seasons in Shimooka, 2003), reflecting differences among sexes such as kinship (Couzin, 2006). Male spider monkeys are philopatric, leading to stronger relationships (Aureli & Schaffner, 2008). Unfortunately, assessments of kinship were beyond the scope of the present study.

Variation in inter-individual distances decreased slightly with increasing fruit availability of the two main food species, suggesting that the response is the result of a passive process related to food availability. Yet, active processes might be at play at the same time. Spider monkeys tend to rest where they have been eating (Parada-López, Valenta, Chapman & Reyna-Hurtado, 2017), and to engage in social activities (e.g., grooming; pers. obs.). If individuals remain for long periods within a given food patch (i.e., typically one large *Ficus* tree or a few clumped *B. alicastrum* trees) carrying out these more sedentary activities, inter-individual distances would be reduced and would likely vary less. For instance, Sugiura et al. (2011) found that in Japanese macaques (*Macaca fuscata*), distances (and associated confidence intervals) between individuals that were resting or grooming decreased relative to individuals that were foraging and moving.

Further studies on social networks considering different spatial scales (i.e., subgroups vs dyads within subgroups at close distances) could provide information on the proximate mechanisms underlying social structure in spider monkeys and other primate species. For instance, proximity patterns at 0 and 5 m varied with time between 2009 and 2014. These changes occurred while variance of fruiting trees, monthly precipitation and monthly temperature remained similar among the three study periods, strengthening support for active processes underlying aggregation. Time was not included as a variable in our study, but changes in proximity patterns might be related to changes in the associations among individuals or to an increase in group size with time (from 27 to 48 individuals), likely leading to constraints in resource access or to changes in the quality of relationships (Goffe et al., 2016). Group tenure, especially for females, could be another factor increasing the association among individuals (see Riveros, Schaffner & Aureli, 2017).

Our study contributes to disentangling how environmental and social factors interact to influence FFD at different scales (subgroup and dyads in the subgroup at close proximity). Spatial aggregations and segregation between individuals were due to both passive and active processes. Some metrics responded to the interplay between fruit availability and the differences between sexes (passive and active processes), while metrics indicating close proximity in dyads reflected sex-related constraints on aggregations (active processes). The effects of fruit availability on association patterns according to sex highlighted the importance of considering differences between sexes in studies of species with high FFD (Aureli & Schaffner 2008, Hartwell et al., 2014). Finally, fruit availability and its variability in time and in space, together with the particular needs of spider monkeys according to their sex, could constitute important selection pressures on the social structure in this species.

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AUTHOR'S CONTRIBUTION

A.R.A.M. designed the research with the help of SC. and GRF. ARAM, BPG, and SESA. prepared the databases. ARAM and SESA performed the analyses with the help of BPG, SC and GRF. All the authors contributed to the interpretation of the data at different levels. ARAM wrote most part of the manuscript, and SC, BPG, SESA and GRF contributed with critical revisions and specific sections.

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CHAPTER 5

GENERAL DISCUSSION AND CONCLUSION

5.1 Context

The principal interest of my thesis was to disentangle the relative influence of environmental and social variables related to the Fission-fusion dynamics in spider monkeys. For this, I worked on three objectives following three baselines around the FFD. These baselines were i) Flexibility of the FFD, ii) Behavioral synchrony as an indicator of group coordination in the FFD, and iii) Passive and active aggregation patterns in the FFD. In the second chapter (Fission-fusion dynamics as a temporally and spatially flexible behavioral strategy in spider monkeys) I tested if the three axes of the FFD (subgroup size, composition and fission rates; Aureli *et al*., 2008) change with rainfall, food availability, and its spatial and temporal variability in two different types of habitat. The responses of the groups in the FFD were sometimes divergent between sites according to spatiotemporal fluctuations in food resource availability. We suggest that these contrasting responses could indicate intra-specific differences in the FFD in the two studied areas with different environmental characteristics. Results of this case study suggest regional differences of the FFD and flexibility of this dynamics at a geographic scale. I showed that subgroup size and fission rates changed with rainfall, food availability and its variability, but those relationships go in contrasting directions depending on the characteristics of the evaluated habitat type (i.e. patches distribution and fruit productivity). However, subgroup composition was stable through the environmental conditions, suggesting a relative tolerance among the individuals of different sexes. Differences related to the differences among sexes and their importance in the FFD were found in the next chapters.

For the third chapter (Environmental and social factors affecting behavioral synchrony in spider monkeys) I used behavioral synchrony as a possible element drawing the fission-fusion dynamics as individuals of a subgroup deal with the ecological and the social environments, and as an indicator of group stability in the FFD. I tested if behavioral synchrony changes under the influence of ecological and social variables, as well as with the monkeys energetic needs during the day and spatial cohesion. I found that small subgroup size and high fruit availability of some tree species are the most important factors permitting behavioral synchrony at the subgroup level. I found as well that homogeneous composition (i.e. individuals of the same sex) and close distances between the individuals are important conditions contributing to the behavioral synchrony at the dyad level. I also showed that it is important to consider synchronization for each activity (i.e. feeding, traveling and resting) because each one responds differently to the environment and the characteristics of a group. Besides, differences in the intrinsic (subgroup size and sexual composition) and extrinsic (fruit availability) characteristics of the studied groups caused differences in the behavioral synchrony.

For the fourth chapter (Fruit availability and social constraints as determinants of association and proximity patterns in the fission-fusion society of spider monkeys (*Ateles geoffroyi*)) I tested how the environmental factors (through passive processes) and sex of individuals (through active processes), influence on the spatial cohesion in the FFD at the subgroup and dyad level. I found that seasonality and fruit availability are important drivers for association patterns. But particularly, phenology and distribution of food species can influence association patterns in different ways. *Brosimum alicastrum* and *Ficus* spp. present contrasting phenology patterns and spatial distribution. Phenology and spatial distribution are important traits in landscape for the FFD (Chapman *et al*., 1995, Sueur *et al*., 2011), so they could give interesting information about the patterns and processes of aggregation in the FFD of spider monkeys. I found that at the subgroup level, association among spider monkeys

reacted mostly to food availability and its variability suggesting a predominance of passive processes; but differences in association patterns by sex showed that active processes also intervene on cohesion patterns. At the dyadic level, with individuals in contact (0m) or at short inter-individual distances (5m) environmental variables barely influenced association between individuals, indicating the importance of social factors on spatial cohesion.

In the next pages I will discuss in more detail the results of the chapters, what is the link between them, and how they are related with the theory presented in the general introduction. I divide the discussion in three subsections that relate the findings of the chapters with some of the principal aspects of living in group and the functioning of the FFD. These subsections are: Spatial cohesion in the FFD, Interplay of ecological and social factors in the FFD, and Diminishing the costs and increasing the benefits in the group. In each of these sections I mention the repercussions and the limitations of this thesis. Finally, I present a general conclusion.

5.2 Spatial cohesion in the FFD

In this thesis I used the definition of subgroup as in Ramos-Fernández (2005), considering all individuals at ≤ 30 m of each other in the same subgroup, and therefore in association. With that, I was able to detect changes in spatial cohesion through the chapters of this thesis. For instance, in chapter 2, spatial cohesion was detected with changes in subgroup size, subgroup composition, and with fission rates; in chapter 3, spatial cohesion was measured by subgroup size; and in chapter 3 and 4 by IIDs. Results show that spatial cohesion, environmental factors, and social factors are inter-related in the FFD in different ways.

In the second chapter, I showed that spatial cohesion in the FFD varies depending on the environment. In that chapter, fission rates changed with ecological variables such as rainfall, fruit availability and variance of fruiting trees, but as mentioned before, with important differences according to the habitat. In the third chapter spatial cohesion was measured through IIDs and it was used as an explanatory variable permitting group coordination. I showed that spatial cohesion is related to social aspects, and the interaction of both can affect group coordination. For example, spatial cohesion and the social factor (proportion of females) were important for changes in behavioral synchronization. Finally, I found that both environmental and social factors can interact to affect the spatial cohesion in the context of association and proximity patterns. Results showed that the ecological and the social factors can affect together the way spider monkeys' associate in subgroups, while social factors are more important for the individuals at close proximities (in dyads). These association patterns were measured through social network analyses metrics, sometimes showing that individuals associate more with individuals of their own sex (Kasper and Voelkl, 2009). Proximity patterns were also tested in chapter 4 using association between individuals at close IID's, and therefore in a strong spatial cohesion. These proximity patterns did not change importantly with the environmental factors suggesting tolerance, affiliation, association preferences and absence of, or low intra-group feeding competition (Whitehead, 2008; Pinter-Wollman *et al*., 2014).

Through this document I show that differences between environments are important to explain spatial cohesion at different levels, revealing as well different information related to association, segregation or coordination. For instance, at a regional scale, we saw that what happen in a habitat, can occur differently in another (e.g. higher fission rates when higher rainfall in a tropical ever-green forest, MABR; but fewer in a medium semi-evergreen forest, OMYK). While at inter-individual scale I saw that spatial cohesion occurs by combination with social factors that can shed light on adaptation in social organisation. Putting together the results of my thesis in relation to spatial

cohesion, I suggest that attraction for resources of interest, firstly shapes aggregation of individuals, but when social aspects appear (e.g. differences between sexes, and social attraction), aggregations form social groups (Whitehead, 2008). For instance, I found that important food patches (i.e. important food species) with a clumped distribution, or that high variability of fruit availability between trees and between species can attract individuals to those common resources. But at the same time, females have more propensity to change their associations, according to changes in food availability and distribution; while males are more stable and have stronger associations.

5.3 Interplay of ecological and social factors on the FFD

Ecological variables influenced the evaluated factors related to the FFD throughout this thesis in different manners, sometimes depending on the different contexts of the environment and on the studied groups' territories. Social variables like subgroup size and sex of the individuals influenced especially behavioral synchrony, and association and proximity patterns. These social variables were also related through social preferences to spatial cohesion as an important element of the FFD.

In relation to the ecological variables, some results support what the ECM says (Chapman *et al*., 1995; Grove, 2012) in the sense that larger food patches and patches with clumped distribution can hold larger subgroups (Grove; 2012). The influence of ecological variables on the FFD has been well documented, and it has been showed that the size, density and distribution of food resources are good predictors of subgroup size (Janson, 1988; Strier, 1992; Chapman *et al*., 1995; Janson and Goldsmith, 1995; Asensio *et al*., 2009; Hartwell et al., 2018) and aggregation patterns (Henzi *et al*., 2009, Ramos-Fernández *et al*., 2009; Cortés-Avizanda et al., 2011; Pinter-Wollman *et al*., 2014). Results about the fission and fusion rates, behavioral synchronization, and

about association patterns, were related in different ways and degrees to what Sueur *et al*. (2011) predict in their theoretical work in relation to the spatial and temporal availability and distribution of food resources. Their predictions included that: i) groups tend to be more cohesive in sites with homogeneous food distribution than in sites with heterogeneous food distribution, ii) FFD will be higher in sites with heterogeneous food distribution until a point where individuals will be more segregated than cohesive so FFD will be low, and iii) FFD will be higher in habitats where temporal variability of food is unpredictable (Sueur *et al*., 2011). However, there are inconsistencies in the way ecological variables influence on subgroup size, and there are fewer studies exploring their relationship with aggregation patterns. Derived from the results in this thesis I suggest that the inconsistencies in the studies relating ecological variables and subgroup membership, and the different results between our study sites and between the studied groups can be related to particular ecological contexts of each environment and even home ranges.

There are important environmental differences in the studied habitats such as rainfall, food tree cross sectional area, food tree basal area, food tree distribution, and food availability. These differences point at the importance of considering the context of the environment when thinking on the ECM and on the influence of food distribution and predictability. For instance, OMYK presented a smaller food tree cross sectional area, food tree basal area, and less rainfall than MABR. Besides, food presented clumped distribution in OMYK and homogeneous distribution in MABR. Hence, FFD is flexible not only for the changes in subgroup membership according to changes in the local environment, but also because of differences at regional scales in the geographical distribution of the species. This could be the case of spider monkeys as they inhabit different types of habitat (lowland rain forest, evergreen, semideciduous, and deciduous forest (Cuarón *et al*., 2008). To approach a broader conclusion about the range of flexibility and the differences in FFD according to the habitat, it would be

necessary to include more groups and study sites. Another option could be realizing more comparative studies between habitats.

Another interesting outcome of this thesis is that some significant food species for the monkey's diet, and their spatial distributions, are important for social organisation. Considering important food species with different spatial distribution and phenology can give important information about FFD. We found that considering important food species for the spider monkeys (e.g. *B. alicastrum* and *Ficus* spp. in OMYK) can help to understand more about association and grouping behavior. For instance, in relation to association patterns, food availability and its variability, and distribution of resources (expressed by *Ficus* spp. and *B. alicastrum*) were essential factors promoting aggregation of spider monkeys. These results were similar to what other studies found (baboons, Henzi *et al*., 2009, spider monkeys, Ramos-Fernández *et al*., 2009; review Pinter-Wollman *et al*., 2014). Studies with migratory birds have found similar results, for instance, Cortés-Avizanda et al., (2011) found that Black kites (*Milvus migrans*) and Egyptian vultures (*Neophron percnopterus*). The mentioned birds are scavengers that when breeding in Europe, where food resources are scarce, are aggregated; while in Sahel, where carcasses are widely available, aggregative behavior is unusual (Cortés-Avizanda *et al*., 2011).

Besides fruit availability of important species, the variability of fruit availability between trees and between different species had an impact on the spatial cohesion, aggregating or dispersing individuals. That information was obtained by the statistical variance of the fruiting trees as an explanatory variable of subgroup size, subgroup composition and fission rates. However, variance of fruiting trees meant different things according to the ecological context of the studied sites. For instance, in both sites (MABR and OMYK) high variance occurred when 20 to 100% of the trees from 30 to 50% of the food species were fruiting; but low variance of fruiting trees meant different things between the study sites. In OMYK, low variance occurred when 10 to 50% of 60% of

the evaluated species presented fruits, while in MABR, low variance occurred when 35% of one species (*Dialium guianense*) was bearing fruits. Still, knowing well their properties and meanings according the contexts, variance of fruiting trees permitted me to visualize the importance of the temporal and spatial variability of food for the regulation of subgroup size, and for association patterns. In this thesis I presented the influence of environmental variables at different temporal and spatial scales on the FFD (e.g. seasonality, availability, variability and distribution of fruiting trees throughout one to three years, and in two different habitats), but adding larger temporal scales would add interesting information on changes in the FFD. For instance, it could permit seeing changes of fruit phenology through years, changes in the animals' diet, and how they are related to the FFD in time.

In the case of the relationship between social factors and the FFD, subgroup size presented a higher impact on behavioral synchrony than fruit availability as an ecological factor. This influence occurred in different ways depending on the activity. Contrastingly to subgroup size, female proportion did not influence significantly behavioral synchrony at the social scale of subgroup, but as mentioned before, probably it was one of the factors (with subgroup size and fruit availability) contributing on the differences in behavioral synchrony between the studied groups. The low influence of the interaction between subgroup composition and fruit availability on behavioral synchrony suggests stability and tolerance among the individuals of different sexes at the subgroup level. Another possibility is that population dynamics (migrations, immigrations, births and deaths) are more important for subgroup composition (Shimooka *et al*., 2008) than fruit availability and its variability. Female-male interactions through time can influence sexual composition (Aureli and Schaffner, 2008). To contrast the influence of population dynamics on the behavioral synchrony variation versus the influence of the female-male interactions through time, we would need longer-term data. Still, influence of social factors on group stability are reflected in the changes of behavioral synchrony between the studied groups. The two studied

groups in MABR presented ecological differences in their home ranges (fruit availability), and differences in their social characteristics (larger subgroups size and female proportion in group A than in B). This condition represents an interesting combination of ecological and social factors influencing group stability.

Sex of the individuals influenced dyadic synchronization and association and proximity patterns reflecting the different requirements between individuals of different sex, and differences in physiological state (Conradt, 1998; Conradt and List, 2009). For instance, same-sex dyads were more synchronized than mixed-sex dyads. Also, the lower synchronization at larger IIDs was more pronounced in mixed-sex dyads than in homogeneous-sex dyads. Exploring in detail differences of activity budgets between sex-classes could help to confirm changes of activity synchronization related to social factors. The tendencies of the synchrony among dyads of the same sex could be related also with the preference of individuals to be more associated with individuals of the same sex. As Watts (2005) states, social preferences could provide opportunities for developing social skills or maintaining alliances.

Throughout the chapters of the thesis I learnt that the strength of associations and social affiliation are important for the spatial cohesion of a group, behavioral synchrony and its stability. Social preferences (Bourgoin *et al*., 2018) or even more homophily (high rates of social interactions among similar individuals; Machado *et al*., 2019) can influence as well spatial cohesion (association and proximity patterns). Kinship could be another important factor influencing spatial cohesion (Sugiura *et al*., 2011; Smith, 2014) and eventually behavioral synchrony. Kin selection could be important for spatial cohesion, because as Smith (2014) says, it can favour social partner choice, coalition formation and social tolerance by withholding aggression. Incorporating information about kinship between the members of the groups, could help us to evaluate the importance of kinship in the FFD. Until now, there is information about kinship in adult and young females thanks to the genealogical recorded data since 1998 in OMYK.

Acquiring genetic data from adult males would be interesting to complete information about kinship in OMYK. The interplay between ecological and social factors on the FFD in chapter 4 was evidenced by changes in the association and proximity patterns. It has been stated that aggregation of animals is due to resources, as food or shelter; while social groups are due to inter-individual forces like recognition and social attraction (Whitehead, 2008). Considering the differences between aggregation of animals and social groups I found that resources and social aspects interact and fluctuate in the FFD of spider monkeys. Some association metrics used in social network analyses permitted to incorporate the sex of the individuals as social factor to see the interplay between the ecological and social factors on the aggregation processes in the FFD (i.e. Modularity by sex, Strength association among females, and Strength association among males). I found, that association patterns (at the subgroup level) responded more (but not only) to environmental factors. I also found a higher association among females (SAF) when fruit availability was more variable between trees and between food species, and at the time of higher fruit availability of the species with uniform distribution and asynchronous in phenology (*Ficus* spp.). Segregation of sexes occurred in rainy seasons when higher fruit availability of the scattered species (*Ficus* spp.), or when fruit availability was more variable between trees and between the food species. In addition, the proximity patterns at the dyad level did not responded significantly or did so very slightly, suggesting impact of social factors like social preferences (Ruckstuhl and Neuhaus, 2000; Bourgoin *et al*., 2018), affiliation (Croft *et al*., 2003; Ramos-Fernandez *et al*., 2009; Goffe *et al*., 2016), homophily (Machado et al., 2019) or kinship (Sueur *et al*., 2010; Smith, 2014). Besides, differences in aggregation patterns related to the ecological variables were different between sexes, probably because of differences in their energetic requirements, in their interests (Conradt and List, 2009).

The main objective of this thesis was to disentangle the influence of ecological and social factors, but during the development of this project, other factors appeared as

possible promoters or regulators of the FFD. One example is time of the day, which is related with the energetic needs of spider monkeys during the course of the day, and therefore indirectly with the biological differences between individuals of different sexes was an important variable only for feeding behavior (Michelena *et al*., 2006; Patzelt, 2011). For instance, feeding synchrony was higher at the beginning of the day in one of the groups, and at the end for other studied group, meaning that this factor interacts with both the ecological and social factors. Including factors like this one in future studies could add useful information on the regulation in the FFD.

5.4 Diminishing the costs and increasing the benefits in groups

All the mentioned interactions between the different factors show until a certain point the complexity of the FFD. Remaining in a group permits individuals to access food, use it efficiently, increase feeding rates while reducing vigilance (Chapman and Chapman, 2000b; Davies *et al*., 2012). But under certain circumstances costs can be higher than the benefits, and one important cost is intra-group feeding competition (Wrangham *et al*., 1993). Intra-group feeding competition can be present as scramble competition, which is the most frequent in spider monkeys (Aureli and Schaffner, 2007), but also and not exclusively as contest competition (Wrangham *et al*., 1993; Davies *et al*., 2012). The ECM, related with the scramble competition hypothesis (Chapman *et al*., 1995; Snaith and Chapman, 2007) states that larger subgroups would travel larger distances to get food resources for all their members until a point where the group will be divided in smaller subgroups to manage better the needs of their members (Chapman *et al*., 1995). My results suggest that a decrease in behavioral synchrony and an increase of fissions occurred when being in the same group impeded individuals to satisfy their needs. The decrease of synchrony in activities could lead eventually to segregation (Calhim *et al*., 2006; Conradt and List, 2009; King and Sueur, 2011).

FFD, as a behavioral strategy could be considered as the practical way groups are continually searching their ideal temporal subgroup sizes as Sibly (1983) suggests. This theoretical subgroup size is related to the cost-benefit dilemma in group size, in which the number of possible competitors foraging has an impact on individual's fitness, leading to changes in the membership of groups (Wrangham *et al*., 1993; Krause and Ruxton, 2002). Subgroup size could also vary with the environment and geographically in the distribution of the species. For instance, Korstjens *et al*. (2006) got an average and a range of subgroup size when considering different populations in the geographical distribution of spider monkeys (3.5, range 3 – 4.8). The range found by Korstjens *et al*., (2006) and the differences in subgroup size in my different chapters, suggest also that that ideal subgroup size could vary geographically in the distribution of species presenting the FFD. According to our results, the average subgroup size also differed between study sites, and even more, between groups. Korstjens *et al*., (2006) found a linear relation between subgroup size and temperature, and a quadratic one with rainfall. Differences between our study groups could be related to what Korsjens *et al*., (2006) say, but the geographical scale and the sample sizes for this thesis do not permits confirm that. However, differences in rainfall are clear between study sites and differences in fruit availability are important between the home ranges of the groups.

A future project in this regard would be to explore how the use of space and the foraging behavior varies with the environment (i.e. fruit availability, patch distribution and habitat), and social factors (i.e. subgroup size, and female proportion). Studies like this have been largely explored through the ECM (Wrangham *et al*., 1993; Chapman *et al*., 1995; Chapman *et al*., 2000). But incorporating data of the different study sites would be helpful considering the contrasting differences of rainfall, food tree patch distribution, fruit availability: and also, differences in subgroup size and composition between the studied groups.

5.5 Conclusion

Life in groups can involve conflicts of interest and compromises between the social and individual needs depending on the environment and changes in it. Spatial cohesiveness, behavioral synchrony and associations among individuals of different sex in a group are related to the intrinsic factors of the group (e.g. group size and sexual composition), and also with the extrinsic factors related to the environment (e.g. food availability in time and space). At the same time, these factors are related because each individual has its own needs in terms of growth, reproduction and energy maintenance to perform its body functions.

This thesis contributes to the knowledge of the FFD as a behavioural strategy of groups to deal with the costs of living in groups and to maintain or increase benefits. Understanding how the ecological and social factors influence FFD provide important information about social, behavioural and ecological adaptations in social mammal, as well as the extent of plasticity of behaviour according to spatio-temporal environmental variations. I explored the influence of environmental and social variables interacting, which is not common, and the few studies using both environmental and social variables have not found consistent patterns. Ecological comparisons between different environments are not frequent in studies with FFD. For the second chapter (Flexibility of the FFD) we developed the study in two contrasting environments in terms of seasonality, rainfall, availability of fruiting trees, and its variability. The third chapter of this thesis was about behavioral synchrony, a study subject common in ruminants, which have high sexual-dimorphism, but not in frugivorous and not highly sexually-dimorphic species presenting a high FFD. In this chapter, results gave some evidence that group size, fruit availability and spatial cohesion are important for behavioral synchronization and indirectly, on the FFD.

In the third (Behavioral synchrony) and fourth chapters (Active and passive processes in the FFD) I incorporated two social scales of analysis (subgroup and dyad) and we found that these two scales give different information. For instance, the dyad scale permitted to appreciate the influence of sex as a social factor determining behavioral synchrony and proximity patterns in the FFD. Subgroup scale permitted to see changes in aggregations of different number of individuals around food resources, considering at the same time the importance of social factors like the sex of the individuals. Results through the thesis suggest that environmental and social variables contribute sometimes in interactions and at different levels on grouping behavior in spider monkeys' FFD. Both factors, the environmental and the social, have an influence on the FFD, but environmental factors influence more aggregation of individuals at the subgroup level; while social factors are more important to shape social groups reflecting social preferences. The last influence is more reflected at the dyad level and at close inter-individual distances.

APPENDICES A

APPENDIX TO CHAPTER 2

A.1 Content:

Table A1. Climatic variables of the two study sites and differences between them.

Climatic variables	Study site		*Z*-value	*P*-value
	OMYK	MABR		
Monthly rainfall (mm)				
Mean	113.4	211.6	93	0.09
Range	1.60 - 421	63.2 - 672.6		
CV	0.07	0.08		
Mean monthly temperature (°C)				
Mean	27.4	25.7	212	0.023
Range	23.0 - 29.8	22.4 - 28.4		
CV	0.071	0.081		
Minimum monthly temperature (°C)				
Mean	21.3	18.9	224.5	0.007
Range	17.4 - 23.9	15.0 - 22.5		
CV	0.094	0.132		
Maximum monthly temperature (°C)				
Mean	33.5	30.24	233.5	0.003
Range	28.5 - 36.8	26.0 - 34.8		
CV	0.066	0.089		

CV: coefficient of variation; *Z*-value: statistic for Wilcoxon signed-rank test between sites.

Table A2. The ten most important food species for spider mokeys at OMYK constituting 85% of the annual consumption between 1997 and 2004 (Pinacho-Guendulain and Ramos-Fernández, 2017); and the eight most important food species for spider mokeys at MABR constituting 57% of the annual consumption between May 2003 and April 2004.

OMYK			MABR		
Scientific name	Local common name	Time spent feeding (%)	Scientific name	Local common name	Time spent feeding (%)
Brosimum alicastrum	Ramón	28.8	*Licania platypus*	Cabeza de mico	17.1
Ficus spp.	Álamo, copó	25.2	*Brosimum alicastrum*	Ramón	13.1
Manilkara zapota	Zapote	7.6	*Ficus* spp.	Higo	6.5
Enterolobium cyclocarpum	Pich	5.6	*Ampelocera hottlei*	Luán, cuerillo	5.3
Guazuma ulmifolia	Pixoy	5.3	*Spondias radlkoferi*	Jobo	4.9
Metopium brownei	Chechén	4.0	*Virola guatemalensis*	Cacao volador	4.9
Spondias mombin	Jujub	3.0	*Guarea glabra*	Cedrillo, Chohalantá	1.2
Talisia olivaeformis	Guaya	2.4	*Dialium guianense*	Guach, palo lacandón	0.8
Sideroxylon foetidissimum gaumeri	Caracolillo	1.7			
Oxandra lanceolata	Botox	1.5			

Table A3. Full generalized linear mixed model of subgroup size of spider monkeys in OMYK and MABR.

Independent variable	Estimate	SE	*Z*-value	*P*-value
(Intercept)	0.331	0.126	2.636	0.008
Site (OMYK)	**1.069**	**0.133**	**8.039**	**0.000**
IFA	**-1.280**	**0.207**	**-6.197**	**0.000**
Variance_ft	**0.233**	**0.048**	**4.852**	**0.000**
Rainfall	**-0.044**	**0.036**	**-1.240**	**0.215**
Site:IFA	**1.400**	**0.209**	**6.687**	**0.000**
Site:Variance_ft	**-0.283**	**0.063**	**-4.504**	**0.000**
IFA:Variance_ft	0.052	0.042	1.250	0.211
Variance_ft:Rainfall	-0.044	0.024	-1.785	0.074
Site:Rainfall	-0.080	0.078	-1.023	0.306
IFA:Rainfall	0.011	0.060	0.187	0.852

* Observation period was included as random effect and all explanatory variables except 'Site' were standardized. Bold variables were those kept in the final model.

Table A4. Results of the full generalized linear mixed model of proportion of females in the spider mokeys subgroups in OMYK and MABR.

Independent variable	Estimate	SE	*Z*-values	*P*-values
(Intercept)	**-0.505**	**0.115**	**-4.411**	**0.000**
Site (OMYK)	**0.048**	**0.133**	**0.359**	**0.720**
IFA	**0.022**	**0.045**	**0.489**	**0.625**
Variance_ft	**-0.091**	**0.033**	**-2.775**	**0.005**
Rainfall	**0.027**	**0.048**	**0.554**	**0.580**
Site:IFA	-0.212	0.251	-0.845	0.398
Site:Variance_ft	0.158	0.092	1.708	0.088
Variance_ft:Rainfall	0.044	0.035	1.245	0.213
Site:Rainfall	-0.184	0.111	-1.650	0.099
IFA:Variance_ft	-0.054	0.061	-0.885	0.376
IFA:Rainfall	-0.060	0.090	-0.675	0.499

* Observation period was included as random effect and all explanatory variables except 'Site' were standardized. Bold variables were those kept in the final model.

Table A5. Results of the full linear mixed model of fission rates in the spider mokeys subgroups in OMYK and MABR.

Independent variable	Estimate	SE	*t*-value	*P*-value
(Intercept)	**0.533**	**0.056**	**9.505**	**0.000**
Site (OMYK)	**-0.061**	**0.069**	**-0.892**	**0.376**
IFA	**0.102**	**0.030**	**3.331**	**0.001**
Variance_ft	**-0.051**	**0.027**	**-1.892**	**0. 063**
Rainfall	**0.120**	**0.032**	**3.797**	**0.000**
Site:Rainfall	**-0.128**	**0.049**	**-2.628**	**0.011**
IFA:Variance_ft	**-0.089**	**0.030**	**-2.933**	**0. 004**
IFA:Rainfall	0.085	0.051	1.673	0.099
Variance_ft:Rainfall	0.027	0.027	0.984	0.329
Site:IFA	0.361	0.316	1.141	0.258
Site:Variance_ft	0.072	0.129	0.562	0.576

* Observation period was included as random effect and all explanatory variables except ‘Site’ were standardized. Bold variables were those kept in the final model.

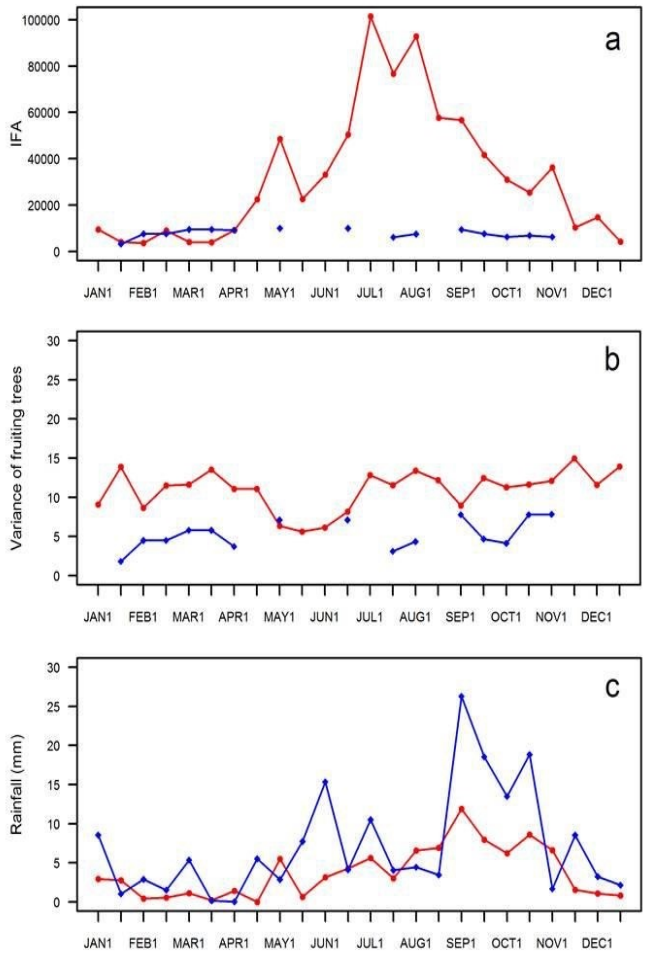

Figure A1. (a) Temporal variation of Fruit availability (IFA), (b) Variance of fruiting trees and (c) Rainfall variation through time in OMYK (red line) and MABR (blue line).

For OMYK, the values of IFA, Variance of fruiting trees, and rainfall were averaged for the two years of data. For MABR, the values of IFA and Variance of fruiting trees were averaged for the areas of two study groups.

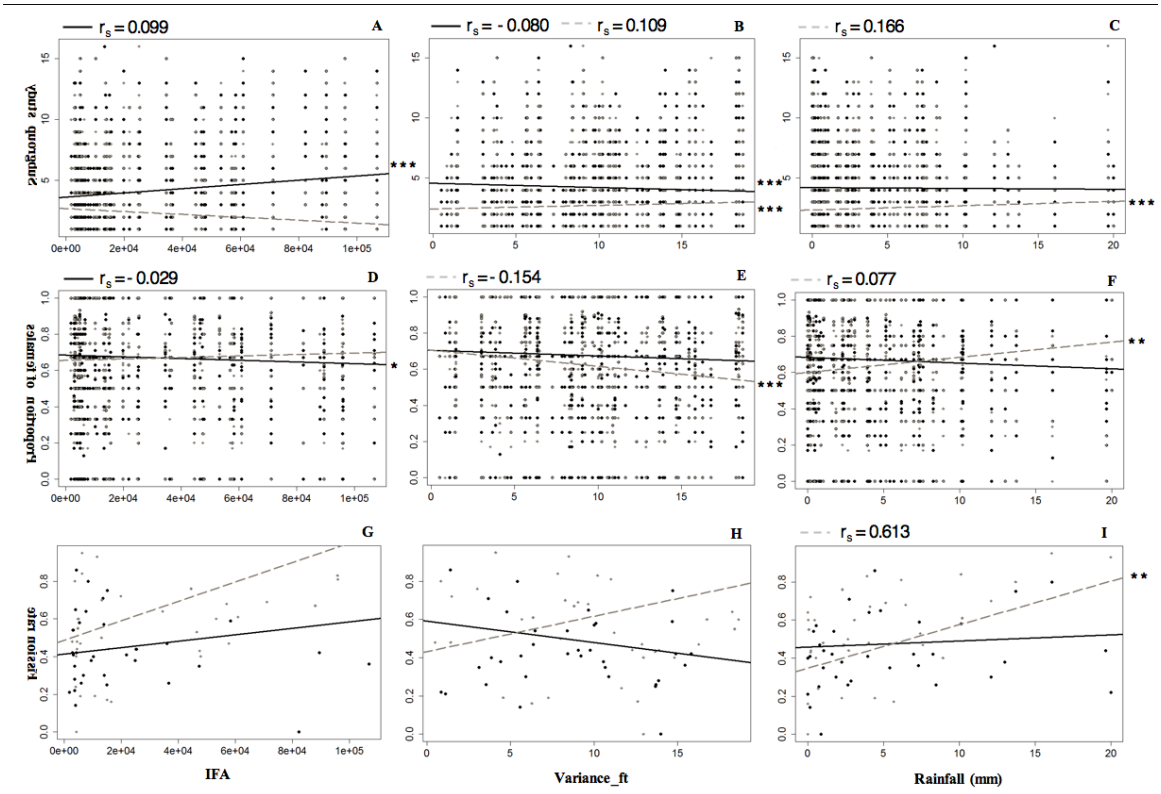

Figure A2. Effect of fruit availability (IFA), Variance of fruiting trees and Rainfall (mm) on the dependent variables through Spearman rank correlations.

A to C show the effects for spider monkey's subgroup size; D to F the effects for Proportion of females; and G to I the effects for fission rate. OMYK (black line and black points) and MABR (gray dashed line and gray points). *** P < 0.001, ** P < 0.01, * P < 0.05.

APPENDICES B

APPENDIX TO CHAPTER 3

B.1 Content:

Table B1. Mean values and differences of the environmental (fruit availability) and social factors (subgroup size and proportion of females) between groups A and B in MABR.

Table B2. Deviations of the best models explaining the relationship between the explicative variables and behavioral synchrony for the objective “Behavioral synchrony related to environmental, social, and internal factors”.

Table B1. Mean values and differences of the environmental (fruit availability) and social factors (subgroup size and proportion of females) between groups A and B in MABR.

Factor	Mean ± SD		Comparison between A and B	
	Group A	Group B	Value	p
Environmental: Fruit availability	9562 ± 4131	5936 ± 3405	T = 190080	**< 0.001**
Social: subgroup size	2.87 ± 1.7	2.46 ± 1.6	T = 433220	**< 0.001**
Social: proportion of females	0.71 ± 0.34	0.59 ± 0.31	Z = 272220	**< 0.001**

Table B2. Deviations of the best models explaining the relationship between the explicative variables and behavioral synchrony for the objective "Behavioral synchrony related to environmental, social, and internal factors".

Response variable	Deviance explained (%)
All activity synchrony	5.1
~ IFA + Subgroup size + Female proportion + Time of day + Group × subgroup size+ Female proportion × group + Group × Time of day	
Feeding synchrony	8.9
~ IFA + Subgroup size + Female proportion + Time of day + Group × IFA + Group × subgroup size + Group × Female proportion + Group × Time of day	
Resting synchrony	6.0
~ IFA + Subgroup size + Female proportion + Time of day + Group × subgroup size + Group × Female proportion + Group × Time of day	
Traveling synchrony	6.8
~ IFA + Subgroup size + Female proportion + Time of day + Group × IFA + Group × subgroup size + IFA × Subgroup size + Subgroup size × Feale proportion + Group × Time of day	

APPENDICES C

APPENDIX TO CHAPTER 4

C.1 Content:

corresponds to the dyads composed by males (m-m), red line corresponds to the dyads composed by females (f-f), and green line correspond to the dyads composed by females and males (f-m).

Figure C2. Contrast plot showing the effect of Variance of fruiting trees (Variance_ft) on the Density in spider monkeys at OMYK, according to season: rainy (blue line) and dry (red). Lines represent the estimated effect of the Variance_ft on Density. Shaded areas represent confidence bands.

Figure C3. Conditional plots where values Modularity by sex are shown in a color gradient. A: Effect of IFA_B and IFA_F on Modularity by sex. B: Effect of IFA_B and Variance of Fruiting Trees (Variance-ft) on Modularity by sex.

Figure C4. Conditional plots. A: Effect of Variance_ft and IFA_F on Strength among females. B: Effect of IFA_F and IFA_B on Strength among females. C: Effect of Variance_ft and IFA_B ON Strength among males.

Table C1. The ten most important food species for spider monkeys at OMYK monitored every two weeks along a phenology trail.

		Monthly consumption	
Scientific name	Local common name	1997–2004	August 2009–July 2010
Brosimum alicastrum Sw.	Ramon	30.0 ± 15.8	29.1 ± 26.3
Enterolobium cyclocarpum (Jacq.) Griseb.	Pich	7.1 ± 13.5	1.8 ± 4.1
Ficus spp.	Álamo, copó	11.65 ± 6.7	5.5 ± 7.4
Guazuma ulmifolia Lam.	Pixoy	5.6 ± 8.5	10.7 ± 20.2
Manikara zapota (L.) P. Royen.	Zapote	8.4 ± 7.4	11.9 ± 15.7
Metopium brownei (Jacq.) Urb.	Chechén	4.3 ± 8.0	3.8 ± 9.6
Oxandra lanceolata (Sw.) Baill.	Botox	2.0 ± 4.1	10.6 ± 24.0
Sideroxylon foetidissimum gaumeri (Pittier) T.D. Penn.	Caracolillo	1.6 ± 2.8	5.2 ± 10.3
Spondias mombin L.	Jujub	2.2 ± 4.6	0.1 ± 0.2
Talisia olivaeformis (Kunth) Radlk.	Guaya	3.5 ± 4.7	4.5 ± 12.3

* Species are listed in alphabetical order. Based on Pinacho-Guendulain & Ramos-Fernández (2017).

Table C2. Definitions of Social Network Analysis terms used in this study.

Term	Definition
Association	Refers to the simultaneous presence of individuals in a same subgroup in a given instantaneous sample. It can also be interpreted as "within range of communication" (Whitehead 2008). These associations gave place to the association patterns of this study, which are: 1) Association Index (AI), 2) Modularity by sex, 3) Network density, 4) Strength of Association among Females, and 5) Strength of Association among Males
Modularity	A topological property of a network and a measure for graph clustering (Brandes et al. 2008). It measures the degree of fragmentation of a group into subgroups of a given characteristic (e.g. age or sex) by comparing interaction frequencies within and between those subgroups (Kasper and Voelkl 2009). A modular pattern consists of densely connected individuals that present a given characteristic, with sparse connections to individuals with other characteristics.
Modularity by sex	Quantifies the presence of same-sex modules within the network to measure individual segregation by sex.
Network density	Represents the tendency of individuals to form social ties (Madden et al. 2009). Density values range from 0 to 1, with high scores indicating 'saturated' networks (all possible ties are present, most individuals are interacting with the majority of all the other individuals), and low scores indicating 'sparse' networks (Madden et al. 2009). If all associates of an individual are themselves linked, then the clustering coefficient of that individual is 1.0; if none of them is linked, the clustering coefficient is 0.0 (Whitehead 2008).
Proximity	Refers to the inter-individual distances (IID) between pairs of individuals in a same subgroup. In this study proximity patterns were given by three variables: 1) P0, i.e. association between a pair of individuals in contact (inter-individual distance = 0 m); 2) P5, i.e. association between a pair of individuals located 3 to 7 m apart; and 3) CVI_IID, i.e. the coefficient of variation of all IIDs occurred in a determined observation period.

Term	Definition
Strength	Refers to the vertex strength centrality in Kasper and Voelkl (2009). The strength is a metrics weighted by the frequencies of association that indicates how much individuals are associated, and how it differs (based on Kasper and Voelkl, 2009).
Strength of Association among Females (SAF)	Indicates how much females are associated to other females.
Strength of Association among Males (SAM)	Indicates how much males are associated to other males.

* Table C2. Terms are presented in alphabetical order.

Table C3. Full linear mixed model of AI at OMYK.

	AI			
Independent variable	Estimate	SE	Z	*P*-value
(Intercept)	-2.325	0.112	-20.682	0.002×10^{-18}
Rain	0.122	0.042	2.928	0.003
IFA_F	0.012	0.011	1.080	0.280
IFA_B	-0.001	0.028	-0.054	0.957
Variance_ft	0.067	0.022	3.073	0.002
Female-male	-0.301	0.100	-3.057	0.002
Male-male	0.187	0.177	1.060	0.289
Rain x IFA_F	-0.039	0.030	-1.301	0.193
Rain x FA_B	**0.275**	**0.034**	**8.007**	**0.118×10^{-16}**
Rain x Variance_ft	**-0.335**	**0.030**	**-11.316**	**0.002×10^{-18}**
IFA_F x IFA_B	**0.173**	**0.011**	**15.860**	**0.002×10^{-18}**
IFA_F x Variance_ft	**-0.125**	**0.012**	**-10.579**	**0.002×10^{-18}**
IFA_B x Variance_ft	-0.012	0.020	-0.591	0.554
IFA_F x Female-male	-0.034	0.022	-1.599	0.110
IFA_F x Male-male	-0.028	0.033	-0.852	0.394
IFA_B x Female-male	0.045	0.028	1.591	0.112
IFA_B x Male-male	0.078	0.042	1.865	0.062
Variance_ft x Female-male	-0.033	0.021	-1.551	0.121
Variance_ft x Male-male	**-0.082**	**0.033**	**-2.458**	**0.014**
Rain x Female-male	**-0.209**	**0.042**	**-5.005**	**0.560×10^{-8}**
Rain x Male-male	**-0.255**	**0.068**	**-3.743**	**0.002×10^{-1}**

* Season by year was included as random effect and all explanatory variables, except ´Season´, were standardized. Bold variables were those kept in the final model.

Table C4. Full linear mixed model of network density (Density) in the spider monkey networks of OMYK.

Independent variable	Network Density			
	Estimate	SE	T	CI (95%)
(Intercept)	0.886	0.019	90.630	0.869 - 0.903
Season (Rain)	-0.014	0.015	-0.960	-0.039 - 0.011
IFA_F	-0.005	0.004	-1.329	-0.011 - 0.003
IFA_B	0.007	0.005	1.374	-0.003 - 0.014
Variance-ft	-0.005	0.006	-0.791	-0.008 - 0.011
Rain×IFA_F	0.013	0.010	1.325	-0.010 - 0.031
Rain×IFA_B	0.012	0.012	1.009	-0.011 - 0.024
Rain×Variance-ft	**-0.013**	**0.009**	**-1.485**	**-0.032 - -0.003**
IFA_F×IFA_B	-0.005	0.005	-0.884	-0.011 - 0.016
IFA_F×Variance-ft	-0.001	0.004	0.381	-0.005 - 0.007
IFA_B×Variance-ft	-0.001	0.007	-0.142	-0.009 - 0.009

* Season by year was included as random effect and all explanatory variables, except ´Season´, were standardized. Bold variables were those kept in the final model.

Table C5. Full linear mixed model of network modularity by sex (Mod_Sex; Newman and Girvan, 2004) in spider monkey networks at OMYK.

	Mod_Sex					
Independent variable	Estimate	SE	T	CI (95%)		
(Intercept)	0.127	0.021	6.085	0.093	-	0.161
Season (Rain)	0.043	0.033	1.307	-0.012	-	0.096
IFA_F	**-0.039**	**0.019**	**-2.111**	**-0.071**	**-**	**-0.003**
IFA_B	-0.010	0.015	-0.678	-0.036	-	0.017
Variance-ft	**-0.033**	**0.023**	**-1.453**	**-0.078**	**-**	**0.004**
Rain×IFA_F	**0.083**	**0.029**	**2.852**	**0.027**	**-**	**0.133**
Rain×IFA_B	-0.010	0.034	-0.287	-0.062	-	0.060
Rain×Variance-ft	**0.069**	**0.032**	**2.185**	**0.014**	**-**	**0.131**
IFA_F×IFA_B	**-0.035**	**0.014**	**-2.494**	**-0.062**	**-**	**-0.009**
IFA_F×Variance-ft	0.003	0.012	0.258	-0.020	-	0.024
IFA_B×Variance-ft	**-0.041**	**0.018**	**-2.278**	**-0.076**	**-**	**-0.010**

* Season by year was included as random effect and all explanatory variables, except ´Season´, were standardized. Bold variables were those kept in the final model.

Table C6. Full linear mixed model of Strength Association among Females (SAF) in spider monkeys at OMYK.

Independent variable	SAF			
	Estimate	S.E.	T	CI (95%)
(Intercept)	0.201	0.035	7.723	0.134 - 0.268
Season (Rain)	0.035	0.045	0.765	-0.053 - 0.123
IFA_F	**-0.022**	**0.004**	**-5.223**	**-0.030 - -0.014**
IFA_B	**-0.034**	**0.005**	**-6.702**	**-0.043 - -0.023**
Variance-ft	**0.027**	**0.006**	**4.745**	**0.016 - 0.039**
Rain×IFA_F	-0.006	0.011	-0.604	-0.028 - 0.014
Rain×IFA_B	0.012	0.011	1.102	-0.009 - 0.033
Rain×Variance-ft	**-0.038**	**0.009**	**-4.312**	**-0.055 - -0.021**
IFA_F×IFA_B	**0.018**	**0.004**	**4.175**	**0.010 - 0.027**
IFA_F×Variance-ft	**-0.033**	**0.004**	**-7.798**	**-0.041 - -0.025**
IFA_B×Variance-ft	-0.000	0.006	-0.020	-0.011 - -0.011

* Season by year was included as random effect and all explanatory variables, except ´Season´, were standardized. Bold variables were those kept in the final model.

Table C7. Full linear mixed model of Strength Association among Males (SAM) in spider monkeys at OMYK

Independent variable	SAM			
	Estimate	S.E.	T	CI (95%)
(Intercept)	0.267	0.030	8.795	0.209 - 0.324
Season (Rain)	0.012	0.018	0.668	-0.021 - 0.045
IFA_F	**0.027**	**0.007**	**3.936**	**0.014 - 0.041**
IFA_B	**0.114**	**0.024**	**4.745**	**0.065 - 0.158**
Variance-ft	-0.000	0.002	-0.069	0.003 - 0.003
Rain×IFA_F	-0.026	0.013	-1.922	-0.052 - 0.000
Rain×IFA_B	**-0.037**	**0.015**	**-2.479**	**-0.067 - -0.009**
Rain×Variance-ft	-0.003	0.004	-0.0941	-0.011 - 0.004
IFA_F×IFA_B	-0.020	0.010	-1.912	-0.039 - 0.001
IFA_F×Variance-ft	-0.003	0.002	-1.644	-0.006 - 0.001
IFA_B×Variance-ft	**-0.009**	**0.002**	**-4.511**	**-0.013 - -0.005**

* Season by year was included as random effect and all explanatory variables, except 'Season', were standardized. Bold variables were those kept in the final model.

Table C8. Full linear mixed model of Proximity Index P0 (individuals located 0-2 m apart) in spider monkeys at OMYK.

Independent variable	P0			
	Estimate	SE	Z	*P*-value
(Intercept)	0.079	0.011	7.044	0.187×10^{-12}
Rain	0.010	0.011	0.926	0.3544
IFA_F	-0.002	0.002	-0.757	0.449
IFA_B	-0.003	0.003	-1.247	0.212
Variance_ft	0.004	0.003	1.395	0.163
Female-male	**-0.061**	**0.012**	**-5.299**	**0.116×10^{-07}**
Male-male	**0.045**	**0.019**	**2.362**	**0.018**
RainxFA_F	0.005	0.006	0.722	0.471
RainxFA_B	-0.008	0.007	-1.146	0.252
RainxVariance_ft	0.015	0.008	1.867	0.062
IFA_FxIFA_B	-0.006	0.003	-1.810	0.070
IFA_FxVariance_ft	0.003	0.002	1.476	0.140
IFA_BxVariance_ft	-0.003	0.0042	-0.890	0.374
IFA_FxFemale-male	-0.002	0.004	-0.536	0.592
IFA_FxMale-male	-0.007	0.006	-1.084	0.278
IFA_BxFemale-male	-0.007	0.006	-1.162	0.245
IFA_BxMale-male	0.005	0.008	0.622	0.534
Variance_ftxFemale-male	-0.001	0.005	-0.191	0.849
Variance_ftxMale-male	-0.001	0.007	-0.159	0.874
RainxFemale-male	0.000	0.012	0.028	0.978
RainxMale-male	0.022	0.016	1.333	0.183

* Season by year was included as random effect and all explanatory variables, except 'Season', were standardized. Bold variables were those kept in the final model.

Table C9. Full linear mixed model of Proximity Index P5 (individuals located 3-7 m apart) in spider monkeys at OMYK.

	P5			
Independent variable	Estimate	SE	Z	*P*-value
(Intercept)	0.084	0.013	6.413	0.143×10^{-12}
Rain	0.012	0.015	0.755	0.450
IFA_F	-0.001	0.004	-0.308	0.758
IFA_B	-0.000	0.006	0.040	0.968
Variance_ft	-0.004	0.006	-0.603	0.546
Female-male	**-0.061**	**0.012**	**-5.300**	**0.116×10^{-07}**
Male-male	**0.044**	**0.019**	**2.304**	**0.021**
RainxFA_F	0.005	0.006	0.722	0.472
RainxFA_B	-0.008	0.007	-1.146	0.252
RainxVariance_ft	0.015	0.008	1.867	0.062
IFA_FxIFA_B	-0.006	0.003	-1.810	0.070
IFA_FxVariance_ft	0.003	0.002	1.476	0.140
IFA_BxVariance_ft	-0.003	0.004	-0.890	0.374
IFA_FxFemale-male	-0.002	0.004	-0.536	0.592
IFA_FxMale-male	-0.007	0.006	-1.085	0.278
IFA_BxFemale-male	-0.007	0.006	-1.162	0.245
IFA_BxMale-male	0.005	0.008	0.622	0.534
Variance_ftxFemale-male	-0.001	0.005	-0.191	0.849
Variance_ftxMale-male	-0.001	0.007	-0.159	0.874
RainxFemale-male	0.000	0.012	0.028	0.978
RainxMale-male	0.022	0.016	1.333	0.183

* Season by year was included as random effect and all explanatory variables, except ´Season´, were standardized. Bold variables were those kept in the final model.

Table C10. Full linear mixed model of the coefficient of variation of the inter-individual distances (CV_IID) in spider monkeys at OMYK.

Independent variable	CV_IID				
	Estimate	SE	T	CI (95%)	
(Intercept)	0.804	5.935	13.551	69.484	- 9.124
Season (Rain)	4.014	7.506	0.535	-9.958	- 1.799
IFA_F	**-0.009**	**4.443**	**-2.125**	**-0.018**	**- -0.000**
IFA_B	**-0.009**	**0.000**	**-2.178**	**-0.000**	**- -0.000**
Variance-ft	0.123	0.305	0.404	-0.500	- 0.689
Rain×IFA_F	-0.007	0.009	-0.821	-0.025	- 0.009
Rain×IFA_B	0.000	0.000	0.443	-0.000	- 0.000
Rain×Variance-ft	1.101	0.666	1.654	-0.073	- 2.641
IFA_F×IFA_B	0.000	0.000	0.136	-0.000	- 0.000
IFA_F×Variance-ft	0.000	0.001	0.022	-0.002	- 0.002
IFA_B×Variance-ft	-0.000	0.000	-0.706	-0.000	- 0.000

* Season by year was included as random effect and all explanatory variables, except ´Season´, were standardized. Bold variables were those kept in the final model.

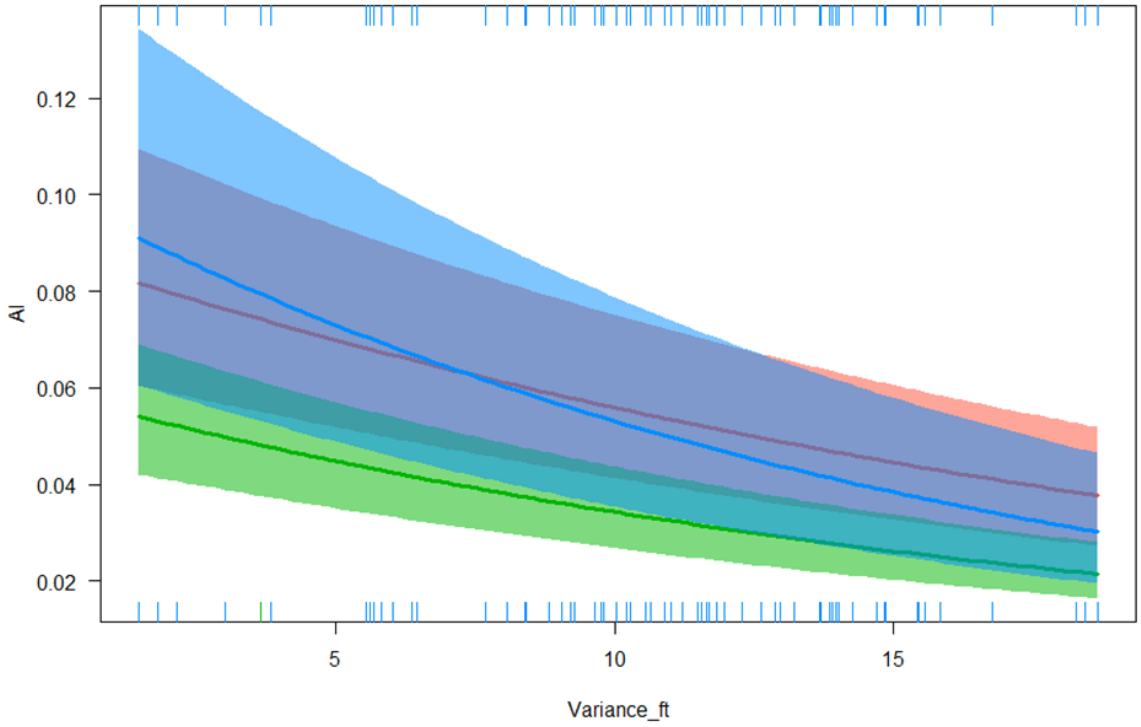

Figure C1. Association Index among spider mokeys in OMYK decreased in all the dyads when the Variance of fruiting trees (Variance_ft) increased.

Blue line corresponds to the dyads composed by males (m-m), red line corresponds to the dyads composed by females (f-f), and green line corresponds to the dyads composed by females and males (f-m).

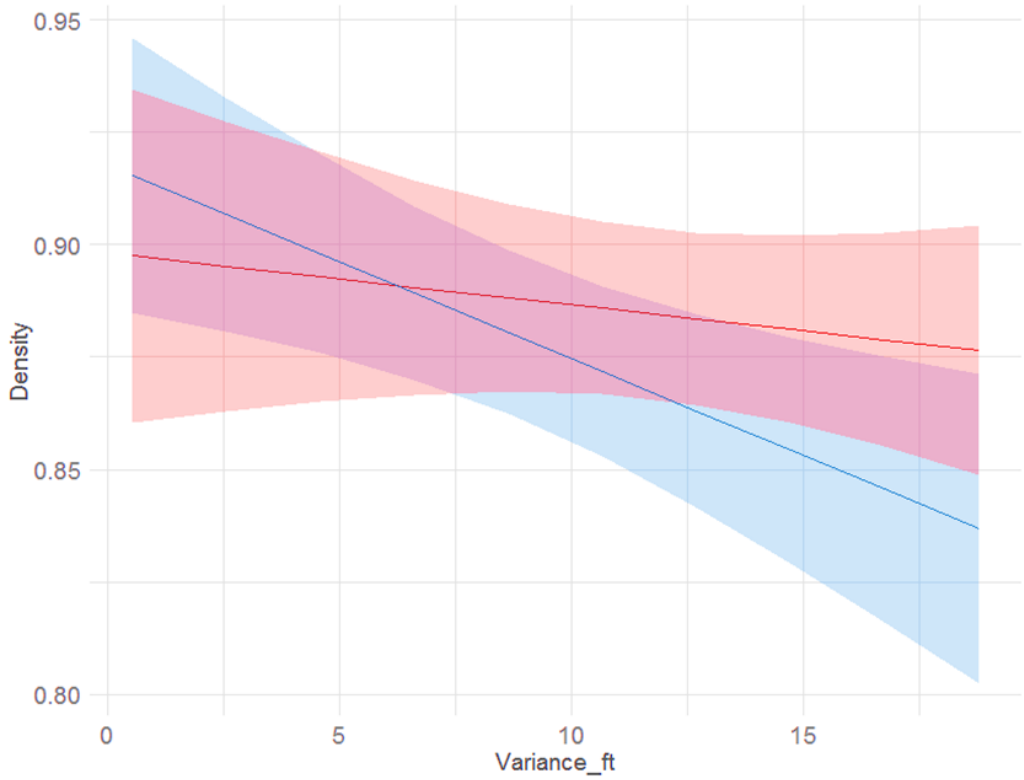

Figure C2. Contrast plot showing the effect of Variance of fruiting trees (Variance_ft) on the Density in spider monkeys at OMYK, according to season:rainy (blue line) and dry (red).

Lines represent the estimated effect of the Variance_ft on Density. Shaded areas represent confidence bands.

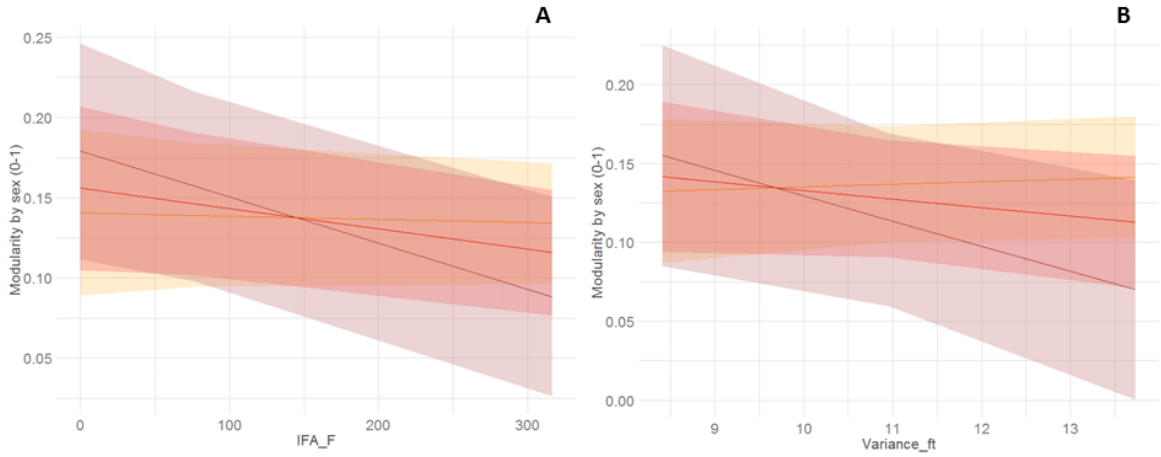

Figure C3. Conditional plots where values Modularity by sex are shown in a color gradient. A: Effect of IFA_B and IFA_F on Modularity by sex. B: Effect on IFA_B and Variance of Fruiting trees (Variance-ft) on Modularity by sex.

Orange line indicates values near the first quartile of IFA_B in A and of IFA_B in B, red line indicates values near the median of IFA_B respectively, and brown line indicates the third quartile. Bands in colors represent the confidence bands.

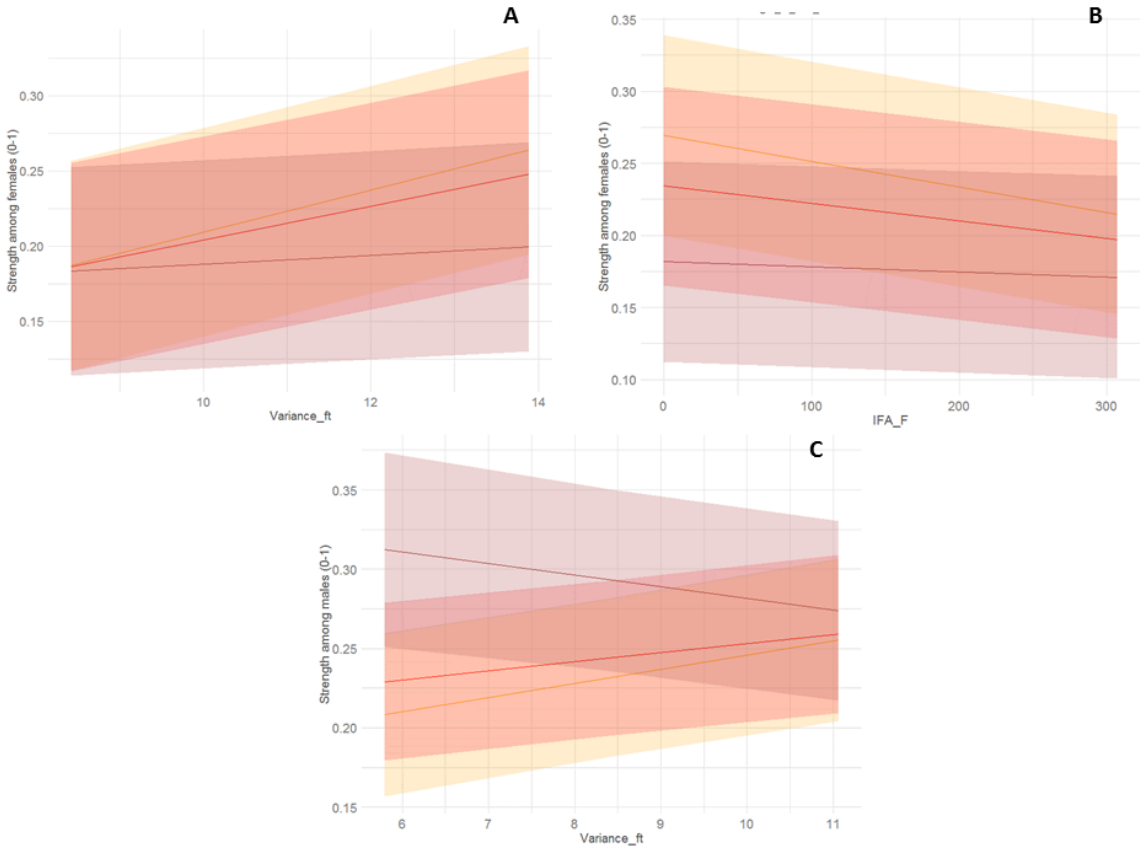

Figure C4. Conditional plots. A: Effect of Variance_ft and IFA_F on Strength among females. B: Effect on IFA_F and IFA_B on Strength among females. C: Effect of Variance_ft and IFA_B on Strength among males.

Orange line indicates values near the first quartile of IFA_F in A, IFA_B in B, and of IFA_B in C, red line indicates values near the median of mentioned variables, and brown line indicates the third quartile. Bands in colors represent the confidence bands.

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